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Effects of water column processes on the use of sediment traps to measure zooplankton non-predatory mortality: a mathematical and empirical assessment

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Complete List of Authors:	Dubovskaya, Olga; Institute of Biophysics of Federal Research Center "Krasnoyarsk Science Center" of Siberian Branch of Russian Academy of Sciences, Laboratory of Experimental Hydroecology; Siberian Federal University, Institute of Fundamental Biology and Biotechnology Tolomeev, Aleksandr; Institute of Biophysics of Federal Research Center "Krasnoyarsk Science Center" of Siberian Branch of Russian Academy of Sciences, Laboratory of Biophysics of Ecosystems Kirillin, Georgiy; Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Department of Experimental Limnology Buseva, Zhanna; Practical Center of the National Academy of Sciences of Belarus for Bioresources, Laboratory of Hydrobiology Gladyshev, M; Institute of Biophysics of Siberian Branch of Russian Academy of Sciences, Laboratory of Experimental Hydroecology; Siberian Federal University, Institute of Fundamental Biology and Biotechnology
Keywords:	zooplankton, Arctodiaptomus salinus, sediment trap, carcasses, stratified lake, non-predatory mortality

Dear Dr. Harris,

Many thanks for the detailed and constructive comments from you and the two reviewers concerning our manuscript.

We have considered these comments very carefully and revised the manuscript accordingly. In relation to Reviewer 1's comments, we have completely over-hauled the manuscript's structure. We now place the study in the context of using sediment trap data to derive zooplankton non-predatory mortality under the condition when processes in addition to sinking (e.g. ingestion, microbial decomposition, turbulent mixing) are important in eliminating carcasses.Dr. Kam W. Tang has made significant contributions in re-interpreting the data and rewriting the manuscript; he is now included as a co-author. In relation to Reviewer 2's comments, we now explain more clearly the mathematical formulations for calculating non-predatory mortality from sediment trap data.

More detailed point-by-point response to the comments are in the following pages.

We hope that this revision has addressed the reviewers' concerns and is acceptable for publication. Please do not hesitate to let us know if you have further comments or suggestions.

Best regards,

Dr. Olga Dubovskaya (corresponding author)

Reviewer(s)' Comments to Author:

Page and line numbers refer to the revision with track change "off"

Reviewer: 1

Comments to the Author

This paper investigates the non-predatory mortality of copepods in a fishless brackish lake using a combination of plankton sampling and sediment trapping, plus an investigation into the physical dynamics of the upper water column that help with interpretation of results.

The subject matter is suitable for JPR and the content of the paper is generally solid. However, I have several substantive concerns and would want to see a major overhaul of the paper before it is considered for publication.

The first concern is about presentation, which normally would not be the first topic in a review but improving clarity may help resolve some of the other issues. There are numerous errors in the use of English, which is understandable; this must be corrected before resubmission but does not materially interfere with reviewing the MS. However, in many places (some identified below) in the MS I found it very difficult to understand what the authors were trying to say. This arose because of poor organization, lack of clarity and consistency in terminology, a superficial treatment of statistical analyses, and vague and subjective treatment of topics such as the role of loss of carcasses within the water column.

>>We have made extensive changes to the manuscript's structure. We now place the study in the context of deriving zooplankton non-predatory mortality rates from sediment trap data when processes in addition to sinking play an important role in eliminating the carcasses. We have extensively edited manuscript, clarified places there were unclear, and improved the language.

We changed the paper title, Introduction (from line 51, page 3), non-predatory mortality estimation in Methods (lines 79-155, pp. 4-6), some parts of Discussion, Conclusion and Abstract (see below). English of the whole MS was checked and improved by Dr Kam W. Tang, who made significant contributions to rewriting the MS. He is now included as a co-author.

The paper is ostensibly about a comparison between two methods of measuring NPM. However, the equations used to develop the basis for analyses are clearly incomplete in lacking a term for losses of carcasses within the water column. Then the Discussion addresses this topic over the course of several pages! A scientific paper is not a mystery novel; key topics should be brought up in the Introduction and addressed throughout. If that were done the manuscript would be far more robust and interesting, as a paper on the importance of predation in loss of carcasses rather than a methodological paper. Such an analysis would also help to explain the concluding sentence in the Abstract, which made no sense to me until I read page 14.

>>We apologize if our manuscript came across as a mystery novel--- that was not our intention. We have now reshaped the manuscript to focus on its main message,such that the study is presented in the context of deriving zooplankton non-predatory mortality rates from sediment trap data when processes in addition to sinking play an important role in eliminating the carcasses. The rationale behind the study is now more clearly explained in the Introduction (lines 58-75, pp.3-4), and the data are discussed accordingly in the Discussion (lines 389-421, pp.13-14; lines 450-503, pp.15-16). We have also shortened the Discussion without sacrificing important details.

It is also not necessary to actually calculate the NPM estimates to see the effect of loss of carcasses on the results. NPM estimates will differ depending on the differences between the two terms yi and y* in the equations. From Figs. 3 and 5, copepods are most abundant at or near the surface, and carcasses are distributed only slightly deeper. Therefore it is clear that y* <yi, and the NPM calculated using y*

will be much less than that using yi. In other words, the comparison in Table 4 is superfluous. Since the difference between these equations is a function of the underlying assumptions, it would seem better to outline in the Methods why one set of assumptions is preferable to the other and then use that method throughout. This would give a clean set of results that would be available for comparison with other findings.

>>Perhaps we did not explain the meaning of the equations clearly enough in the previous version. The obvious fact that $y^* < y_i$ was the starting point of our study, which needed explanation and quantification because it contradicted the common assumptions behind the use of sedimentation trap for NPM estimation.While we agree that one can get a first impression of the effect of carcass loss by observing $y^* < \overline{y}_l$, we think it is important to demonstrate the effect quantitatively, and also to explain the meaning of the trap data when $y^* < \overline{y}_l$ vs. $y^* \geq \overline{y}_l$. To clarify these points, we followed exactly the suggestions of the Reviewer by describing carefully the assumptions behind both approaches in Introduction and by comparison of their outcomes in Discussion. Following the reviewer's suggestion, we have now explained the mathematical derivations and the underlying assumptions more clearly, as well as their meaning for calculating non-predatory mortality. Furthermore, in the revision we explain and quantify the parameters *G* and *D*, which represent the elimination of carcasses by sinking and by water column processes, respectively, shown in Table 5 (p.27, line 705). In this context, the comparison in Table 5 is essential for the presentation of results and should be retained. G and D are described in Results (line 355-358, p.12) and are discussed in Discussion (line 414-421, p.14; line 435, p.15), and the paragraph *Turbulence effect and microbial decomposition* (line 450-503) also discussed processes included in D. We substituted Fig. 5 with Table 4 (p. 26, line 701) with additional data about the difference between y* and $\overline{y}_l$., as $(\overline{y}_i - y_i^*)$ and $(y_i^*/\overline{y}_i)$, which are described in Results (lines 353-355, p.12) and discussed in Discussion (lines 402-413, p.14)

The statistical treatment seems weak. I think there is an overemphasis on statistical testing, with many of the tests having (unstated) trivial null hypotheses. One example is the test of differences in abundance by depth band: the null hypothesis is that the distribution would be uniform, but since the lack of copepods at depth was already established, there would be no good reason to entertain such a null. More generally the aim of this study is to quantify NPM and assess the two methods of calculation, not to test hypotheses.

>> Following the reviewer's suggestion, we have removed some of the text related to statistical testing. We now focus our message on quantifying NPM using sediment trap data when also accounting for carcass removal by water column processes.

Stratification of vertical distribution of live and dead Arctodiaptomus abundance and the fact $y^* < \overline{y}_l$, are obvious from Fig.3 and Table 4 and their description in Results (line 299-310, p. 11).One-way ANOVA revealed in general significant difference between sinking velocities of carcasses of different Arctodiaptomus stages (line 342-346, p.12), and two-way ANOVA revealed the differences between mean sinking velocities of different stages during different time periods which were taken for mortality calculation (line 346-348, p.12). More detailed statistics is redundant and is deleted from the MS.

The first paragraph of the Discussion should be made more rigorous. It is vague, poorly supported, and unclear, and should be replaced by a model-based approach that more convincingly supports its conclusions. Relative error is probably not the best statistic for such a comparison. The same holds for analyses Page 14.

>> We have completely rewritten the Discussion. It now begins with a discussion of the suitability of sediment trap method for studying sinking fluxes (including zooplankton carcasses) (p.13, line 371-387).

We used Relative Errors to confirm that our data from traps and the water column had the same variability as common hydrobiological data (line 393-401, pp.13-14).

Why are maxima and minima used for these analyses? Maxima and minima are inherently not robust.

>>Gammarus predation was estimated as consumption = respiration losses (or daily energy expenditure). The word "minimal" was deleted from the text (line 436-437). However, to estimate maximal possible consumption we took maximal abundance of Gammarus in the water column. This maximal consumption appeared to be more interesting in comparison with difference between y^* and $\bar{y}_l$. The conclusion "ingestion of carcasses by *G. lacustris* within 0-12 m could explain the loss of carcasses" (line 448, p.15) will not change by using average Gammarus abundance in the calculations.

The full paragraph on page 16 is disorganized, very hard to follow and poorly argued and supported. If the random-walk model is unsuitable, it should not be brought up as if it were suitable and then discarded. Some other model might be preferable, but the unsuitability of this model should be explained better.

>> We have completely rewritten the Discussion. The message is not that the random walk model is unsuitable (it is for sure suitable for description of turbulence);the model shows that 'turbulence' in its conventional sense (isotropic, homogeneous, small-scale,viscosity-dominated,Reynolds-type velocity fluctuations) cannot produce any direct effect on particle sinking on time scales essentially longer than those of the turbulent fluctuations. The paragraph is rewritten to make the point clear. (page 16, line 488-498)

The data are based on counts and there are model-fitting procedures specifically for use with count data that allow the researcher to avoid the use of non-parametric methods (which generally give only yes/no answers and are therefore of no use in a study such as this). Such methods, including Poisson and negative binomial regression, are readily available in R and widely used.

>>We intentionally avoided any model-fitting procedures, as they would contradict to the main point of the study, viz. understanding what the sediment trap data deliver with regard to estimation of the zooplankton production-mortality budget.

We used only two Anova with normally distributed data without additional statistics that seemed to be redundant. We deleted a sentence about using non-parametric Kruskal-Wallis test (line 275-276, p. 10).

A good example of the lack of clarity is the terminology used in the equations and to describe the results. The letter y is used for a variety of things: y is carcass abundance by depth and sample, yi is mean carcass abundance above the trap with i apparently signifying sample, y* is the abundance at trap depth, and Y is the catch of the trap over a time interval. I kept having to go back to remind myself which form of y meant what. Sinking rates are variously described with the letters v and w. A table of terms would help but there are many other letters in the Roman and Greek alphabets that could be used for some of these things, and the choices could be made to clarify the meaning for the reader. Moreover, all of these terms have a time (sample) component to them but only yi is so identified.

>>The nomenclature was indeed slightly mixed up and difficult to follow. We have now carefully revised all symbols in order to make them consistent across all derivations (in Methods, line 79-155).

There are many examples of inappropriate words or baffling phrases (page/Line number):

>>The entire text is extensively revised following the reviewer's suggestions.

3/44"turbulence" => "turbulent"

>>Rewritten as suggested.

3/57 "a studying water column"

>>Rewritten.

4/8-10 "estimation…beneath." Unclear

>>Rewritten as suggested.

10/50 "averaged…limits"

>>Rewritten, line 318-319, p.11

11/12 "as well as…" this seems to say that the swimmers in the traps had Gammarus guts in their guts, which I don't think is the intended meaning.

>>Improved as suggested, Line 328-331

14-55 "were similar" Similar to the carcass density I guess, but it should say so.

>>The sentence is deleted.

15/32-33 "Although… effect" No idea what this means.

>>Rewritten, line 471-473, p.16

15/45-46 "laboratory settling column velocity decreased by a factor of two" No it didn't.

>>The sentence is deleted.

16-1 Zero excess density at zero sinking velocity – this is a tautology.

>>Rewritten, line 486-487, p.16

16/39 “poorly”

>>Rewritten

Other specific comments

10/20 Usually when a citation is included it means the statement should be in the Discussion.

>>Citation is moved to Discussion

11/40 “pairs of nauplii and males or …” So pairwise statistical tests were run? What is the null hypothesis, and is it a meaningful one?

>>This statistical analysis is removed.

3/20 spelling of author’s name (and other misspellings)

>>Improved as suggested.

3/32 “sedimentation…decomposition” Clarify the basis for this comparison – presumably the former is a velocity and the latter is a specific rate. In any case “is believed” is rather weak and could be made stronger by a brief statement of what actually has been found in previous studies.

>>Rewritten as suggested.

12/55-56 “or equilibrate…. beneath.” No idea what this means.

>>Rewritten as suggested.

Page and line numbers refer to the revision with track changes “off”

Reviewer: 2

Comments to the Author

The authors present a paper with a lot of field data and mathematical framework for the estimation of non-predation mortality of Arctodiaptomus salinus (Copepoda: Calanoida) in a brackish meromictic Lake Shira (Russia). The methods of sampling, counting, video recording etc. look well. The equations and

mathematical transformations are no doubt. As result the paper seems a good methodological study of complicated estimation of non-predatory aspect of zooplankton mortality.

On the other hand, the main idea of paper is the comparison of two equations. It looks as restricted barrier for study:

First, I think that the comparison of these two equations is impossible.

>> We thank the reviewer for the compliment. Following the editor's and the reviewer's suggestion, we have restructured the manuscript substantially such that it does not appear to be merely about method (equation) comparison. Instead, we place the study in the context of deriving zooplankton non-predatory mortality rates from sediment trap data when processes in addition to sinking play an important role in eliminating the carcasses.Furthermore, in the revision we explain and quantify the parameters G and D, which respectively represent the elimination of carcasses by sinking and by water column processes.

G and D are given in Table 5 and described in Results (line 355-348, p.12) and are discussed in Discussion (line 414-421, p.14, line 435, p.15).The paragraph *Turbulence effect and microbial decomposition* (line 450-) also discussed processes included in D. We substituted Fig. 5 with Table 4 (p. 26, line 701) with additional data about difference between y* and $\overline{y}_i$., as ($\overline{y}_i - y_i^*$) and ($y_i^*/\overline{y}_i$), which are described in Results (lines 353-355, p.12) and discussed in Discussion (lines 402-413, p.14)

It is clear that Eq. 8 estimates NPM of C5 stage because copepodities C5 only congregated near trap position (Figs 3, 5). However, Eq. 6 estimates NPM of whole population. The comparison of the results of these two equations is not good way.

>>The NPM calculation is affected by carcass distribution within the water column. In the revision, we calculate NPM using the different formulations (Line 79-155 in Methods) for all the available developmental stages, and not just C5 (Table 5). Furthermore, in the revision we explain and quantify the parameters G and D for the different developmental stages, which respectively represent the elimination of carcasses by sinking and by water column processes (see above page, line) The revision should provide readers with a fuller view of the calculation and interpretation of stage-specific NPM.

Second, it seems that the Eq. 6 determines NPM well if the population has homogenous vertical distribution. However, the stages of Arctodiaptomussalinus have pronounced unstable different positions in water depth (Fig. 3). There is reasonable doubt that Eq. 6 is suitable in this case.

>> As explained above, we calculate NPM using the different formulations for all the available developmental stages (Table 5). We also quantify the parameters G and D presenting the elimination of carcasses by sinking and by water column processes, respectively (see above page, line). We also compare our NPM estimates with literature data to assess their validity. This revision should therefore provide readers with a fuller view of NPM calculation and interpretation of the data (Line 539-547 – Conclusion)

My suggestions are:

1. The comparison of two equations should be excluded from paper.

It is possible to use Eq. 8 as an example for estimation NPM of separate stage of copepodities.

>> We feel that both equations are needed in order to explain the effect due to different carcass elimination processes. We have restructured the manuscript substantially such that it does not appear to be merely about method (equation) comparison. Instead, we place the study in the context of deriving zooplankton non-predatory mortality rates from sediment trap data when processes in addition to sinking play an important role in eliminating the carcasses (Introduction, line 58-75, Methods, line 79-155, Discussion).

2. It would be useful for the reader if the authors add at least small review of papers with the formulas of NPM and its parameter's estimations.

This review can present the scale of main idea of paper.

>> In the Introduction, we have now included a literature review of NPM, its estimations and ecological consequences. This will help readers to put our study in a broader ecological context (page 3, line 41-68).

3. I am very surprised to see a lot of equations in Discussion.

It seems to be better to separate the equations from «Reality check of non-predation mortality estimates» and to write a new paragraph in Methods.

>> We have now shortened the Discussion and moved the relevant equations to the extended 'Methods' section (line 79-155). We also have shortened the subsection "Reality check of non-predatory mortality estimates" and focused on comparing our values with literature mortality values (page17, line 514-531)

Specific additional comments

>> We have revised the text extensively as suggested.

Page 2, line 30:

Keyword "non-predation" should be replaced by "non-predatory".

>> Changes made throughout the manuscript as suggested.

Page 8, line 35:

The authors write about the layer from 12 m to surface for obtaining the values of parameters Ni and yi.

However, they write about the layer 0-15 m for these parameters on page 12, line 52 and page 34, line 47.

Which depth is correct?

>>We clarified this in line 213-214 and line 236-242 of Methods. NPM was calculated in the whole water column 0-15 m with using $\overline{N}_i$, $\overline{y}_i$, and $\overline{y}_{i+1}$ for this layer, these characteristics were calculated with using data from 0-12 m.

Page 13, line 50:

A subscript "i" is missed for parameter y.

>>All nomenclature is checked and corrected.

Page 22, lines 1 – 9:

Double reference

>>We have revised the text following the reviewer's suggestions

Page 16, line 17 and page 23, line 25:

McDonell or McDonnell?

>>Changed to McDonnell

Page 16, line 20 and page 23, line 29:

McDonell or McDonnell?

>>Changed to McDonnell

Page 15, lines 50, 54 and page 23, line 57:

Svetlichny or Svetlichnyyi?

>>Changed as in the cited literature

Page 7, line 12 and page 24, line 19:

Tolomeyev or Tolomeev?

>>Changed as in the cited literature

Page 14, line 50 and page 24, line 19:

Tolomeyev or Tolomeev?

>>Changed as in the cited literature

Page 14, lines 40-42 and page 24, line 45:

Tolomeyev or Tolomeev?

>>Changed as in the cited literature

Page 17, line 59:

I can't understand last sentence.

It seems that you should use the term "carcasses elimination" instead of the term "carcasses production".

>>Rewritten as suggested.

Page 31, line 51:

A comma is missed between "temperature" and "salinity".

>>Improved as suggested.

Effects of water column processes on the use of sediment traps to measure zooplankton non-predatory mortality: a mathematical and empirical assessment

Olga P. Dubovskaya[1,2*], Aleksandr P. Tolomeev[1], Georgiy Kirillin[3], Zhanna Buseva[4], Kam W. Tang[5], MichailI. Gladyshev[1,2]

1 Institute of Biophysics of Federal Research Center "Krasnoyarsk Science Center" of Siberian Branch of Russian Academy of Sciences, 50/50 Akademgorodok, Krasnoyarsk, 660036, Russia,

2 Siberian Federal University, 79 Svobodny avenue, Krasnoyarsk, 660041, Russia,

3 Department of Ecohydrology, Leibniz-institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, Berlin, 12587, Germany

4 Practical Center of the National Academy of Sciences of Belarus for Bioresources, 27 Akademicheskaya Street, 220072, Minsk, Belarus

5 Department of Biosciences, Swansea University, SA2 8PP, U.K.

* corresponding author e-mail: dubovskaya@ibp.krasn.ru

Running head: Zooplankton non-predatory mortality

Keywords: zooplankton, *Arctodiaptomus salinus*, non-predatory mortality, sediment trap, carcasses, stratified lake

Abstract

Zooplankton populations can at times suffer mass mortality due to non-predatory mortality (NPM) factors, and the resulting carcasses can be captured by sediment traps to estimate NPM rate. This approach assumes sinking to be the primary process in removing carcasses, but in reality carcasses can also be removed by ingestion, turbulent mixing and microbial degradation in the water column. We presented mathematical formulations to calculate NPM from sediment trap data by accounting for carcass removal by processes in addition to sinking, and demonstrated their application in a field study in Lake Shira. Carcass abundance of the major calanoid copepod *Arctodiaptomus salinus* decreased with depth, indicating the effect of carcass removal from the water column. The estimated NPM values were comparable to physiological death rates reported in the literature. We further used independent data to partition carcass removal into detritivory, turbulent mixing and microbial degradation. Estimated ingestion by the amphipod *Gammarus lacustris* could account for the disappearance of copepod carcasses above the traps. Wind-driven currents and turbulence could also extend the carcass exposure time to microbial degradation. Collectively, these water column processes would facilitate the remineralization of carcasses in the water column, and diminish the carcass carbon flux to the benthos.

Introduction

Zooplankton population dynamics is determined by two fundamental processes: Birth and death. In contrast to birth rate, estimation of *in situ* zooplankton mortality is logistically challenging (Dubovskaya, 2009; Tang and Elliott, 2013;Kimmerer, 2015). Apart from predation, zooplankton can suffer non-predatory mortality (NPM) such as senescence, environmental stresses, food limitation, diseases and parasitism (Tang et al., 2014), and leave behind carcasses. The importance of NPM in constraining zooplankton population growth has been demonstrated theoretically (Gentleman and Head, 2017) and empirically (Elliott and Tang, 2011). It can account for on average 25-33% of the total mortality among epi-pelagic marine copepods (Hirst and Kiørboe, 2002; Elliott and Tang, 2011); in some cases, NPM is the main cause of zooplankton population collapse (e.g. Gries and Gude, 1999; Dubovskaya et al., 2003; Wagner et al., 2004).

Sediment traps are widely used to collect sinking matter for characterization and to quantify sinking fluxes (Buesseler et al., 2007), and appearance of zooplankton carcasses (distinguishable from swimmers) in sediment traps indicates the role of sinking in removing zooplankton carcasses from the water column (Frangoulis et al., 2011;Dubovskaya et al., 2015). Several sediment trap studies have highlighted the contribution of zooplankton carcasses to the carbon sinking flux (Sampei et al., 2009, 2012; Ivory et al., 2014); sediment trap data also have been used to estimate carcass sinking rates and NPM (Dubovskaya et al., 2015).

In addition to sinking, zooplankton carcasses can be removed by a multitude of water column processes such as microbial decomposition, detritivory and turbulent mixing before the carcasses reach the traps (Dubovskaya, 2008; Elliott et al., 2010; Kirillin et al., 2012).Indeed, a decrease in carcass abundance with depth has been reported (e.g., Bickel et al., 2008). Therefore, proper calculation of NPM requires knowledge of both the mean carcass abundance in the water column above the sediment trap ($\bar{y}$) and carcass abundance at sediment trap depth (y^*). By comparing $\bar{y}$ and y^*, we can also gain insights into the relative importance of sinking vs. other removal processes in controlling the fate of zooplankton carcasses. In the simplest terms, we can consider two scenarios: (i) $\bar{y} \leq y^*$ suggests sinking dominates over other processes in removing carcasses from the water column; (ii) $\bar{y} > y^*$ suggests other processes are also important in removing carcasses (see Methods section for details).

Here we use Lake Shira, a fishless brackish meromictic lake in Russia, as a model system to study in situ NPM and carcass dynamics of the dominant species *Arctodiaptomus salinus* (Copepoda: Calanoida). The objectives were to estimate NPM from sediment trap data and investigate the relative importance of sinking vs. other removal processes—encapsulated by the removal coefficient D—in controlling carcass dynamics in the water column. We further attempted

to partition D by independently estimating microbial degradation, turbulent resuspension, and detritivory by the dominant invertebrate predators.

Methods

Non-predatory mortality estimation

In situ NPM estimations are based on the equation of vertical transport with a source term in the following form:

$$\frac{\partial y}{\partial t} = mN - \frac{\partial F}{\partial z}, \quad (1)$$

where m (d^{-1}) is the specific non-predatory mortality, F is the vertical flux of carcasses, N and y are abundances of live individuals and carcasses (ind m^{-3}), respectively. Integration of this equation over the layer $0 < z < h$ above the sediment trap, under the assumption of zero flux of the carcasses across the air-water boundary $F(0) = 0$, yields:

$$\frac{\partial \overline{y}}{\partial t} + \frac{F^*}{h} = \overline{mN}, \quad (2)$$

where the overbar means averaging over the water column $0 < z < h$; the vertical flux F^* of carcasses at the trap exposure depth h (ind m^{-2} d^{-1}) is directly measured by sediment traps as

$$F^* \equiv v^* y^* = \frac{Y}{S}, \quad (3)$$

and

$$v^* = Y/(Sy^*). \quad (4)$$

Here, Y is number of carcasses accumulated in a sediment trap per day (ind d^{-1}), S is the input area of the trap (m^2), v^* (m d^{-1}) and y^* (ind m^{-3}) are the sinking velocity of carcasses and the concentration of the carcasses at trap exposure depth (i.e. outside the trap), respectively. The final expression of the non-predatory specific mortality m becomes

$$m = \frac{1}{\overline{N}}\left(\frac{\partial \overline{y}}{\partial t} + Gy^*\right), \quad (5)$$

subject to subsequent integration with respect to time based on discrete series of measurements on y^* and v^*. Here,

$$G = \frac{v^*}{h} \quad (6)$$

is the specific rate of elimination of carcasses from the water column via sinking. In order to explore the application of Eq. 1and Eq. 5 to estimate NPM, we consider a simple case of depth-constant sinking velocity v. Then, Eq. 1 becomes

$$\frac{\partial y}{\partial t} = mN - v\frac{\partial y}{\partial z}. \quad (7)$$

Assuming further that the live zooplankton are homogeneously distributed throughout the water column (N=constant), and the situation is close to steady state ($\partial y/\partial t \approx 0$), Eq. 1 is solved as

$$y = (mN/v^*)z + y_{0,} \quad (8)$$

i.e. abundance of carcasses y should increase linearly with depth unless they are removed before reaching the trap. This equation however does not take into account various processes other than sinking, such as turbulence, degradation and detritivory, in removing carcasses from the water column. The combined effect of these processes can be represented by adding a first-order removal rate with a coefficient D to Eq. 1:

$$\frac{\partial y}{\partial t} = mN - v\frac{\partial y}{\partial z} - Dy. \quad (9)$$

In contrast to Eq. 8, solution to Eq. 9 yields exponentially decaying carcass abundance y with depth. To explore its effect on m, we assume the instantaneous carcass abundance is proportional to the abundance of live zooplankton, $y = \delta N$. The analytical solution to Eq. 9 under the same assumptions N = constant and $\partial y/\partial t \approx 0$ is

$$y(z) = y_0 \exp\left(\frac{m - D\delta}{\delta v} z\right), \quad (10)$$

and the solution with respect to m, analogous to Eq. 5 can be written as

$$m = \frac{1}{\bar{N}}\frac{\partial \bar{y}}{\partial t} + \frac{1}{\bar{N}}\left(D\bar{y} + Gy^*\right). \quad (11)$$

Thus, the mortality rate m_{trap} calculated from sediment trap data is reduced by relative loss rate, as compared with the real mortality *in situ*:

$$m_{trap} = m - D\frac{\bar{y}}{\bar{N}}. \quad (12)$$

Hence, at high removal rate D, carcass abundance at trap depth (y^*) approaches zero, and estimations of mortality from Eq. 5 become unreliable. Its alternative, Eq. 11 requires empirical measurement of D by extensive sampling and analysis of the plankton communities, which is logistically challenging to do in parallel to *in situ* trap measurements. A practical alternative is by adopting the integral sample of carcasses abundance over the entire water column as an approximate of their abundance at the trap deployment depth, i.e. $\bar{y} \approx y^*$, which turns Eq. 5 to:

$$m = \frac{1}{\bar{N}}\left(\frac{\partial \bar{y}}{\partial t} + G\bar{y}\right) \quad (13)$$

This formulation was used for NPM estimations by Gladyshev and Gubanov (1996) (see also Gladyshev et al., 2003).

By comparing Eq. 13 and Eq. 5; i.e. replacing y^* with $\overline{y}$, we can estimate the variance in m caused by elimination of carcasses above the trap depth. For example, introducing $\gamma = (D–m/\delta)/v$, one can show that $\overline{y}/y^* \to 1$ at $\gamma h \to 0$, and $\overline{y}/y^* \to \infty$ at $\gamma h \to \infty$, where h, as before, is the depth of the trap exposition. Hence, Eqs.5 and 13 are interchangeable if the traps are positioned close to the depth of the maximum abundance of zooplankton (Dubovskaya et al., 2015), and the error becomes higher with deeper exposition of traps. An intermediate case $\gamma h \approx 1$ yields $\overline{y}/y^* \approx (e-1) \approx 1.71$, i.e. Eq. 13 would in typical configurations slightly overestimate the mortality rate, but the overestimation is within the range of method accuracy. Eq. 13 becomes equivalent to Eq. 11 if

$$D = G\left(1 - \frac{y^*}{\overline{y}}\right). \quad (14)$$

Hence, *in situ* mortality rates as produced by Eq.13 imply a depth- and time-constant elimination of carcasses at the rate given by Eq. 14. At small y*, Eq. 14 suggests that the elimination of carcasses above the trap is nearly equal in magnitude to the removal of carcasses due to sinking:

$$D \approx G. \quad (15)$$

For estimation of the NPM from discrete sampling, a finite difference equivalent of Eq. 13 is used:

$$m_i = \frac{\Delta\overline{y}}{\Delta t \cdot \overline{N}_i} + G_i \cdot \frac{\overline{y}_i}{\overline{N}_i} \quad (16)$$

Where m_i (d^{-1}) is the specific NPM at the time t_i (day), $\Delta t_i = t_{i+1} - t_i$, is the period between two sampling events i, $\overline{y}_i$ is the mean abundance of carcasses (ind.·m^{-3}) at t_i in the water column above the trap, $\Delta\overline{y} = \overline{y}_{i+1} - \overline{y}_i$, $\overline{N}_i$ is abundance of live individuals (ind.·m^{-3}) in the water column above the trap. Eq. 5 becomes:

$$m_i = \frac{\Delta\overline{y}}{\Delta t \cdot \overline{N}_i} + G_i \cdot \frac{y_i^*}{\overline{N}_i} \quad (17).$$

The difference between Eq.16 and Eq. 17 is in using $\overline{y}$ vs. y^* in the last term. In the following we applied both Eq. 16 and Eq. 17 to estimate zooplankton NPM in Lake Shira, and to evaluate the relative importance of D vs. G.

Study site

Lake Shira (54.499°N, 90.204° E), situated in the steppe area of Khakassia Republic at 354 m above sea level, has been intensively studied for the last 2 decades (Zotina et al., 1999; Yemelyanova et al., 2002; Rogozin et al., 2010, 2016; see also special issues of Aquatic ecology 2002, 36 (2) and 2010, 44 (3)). The lake area is 35.9 km^2, the maximum depth is 24 m. The depth of

the upper boundary of the anoxic monimolimnion with hydrogen sulfide varies seasonally and annually (Rogozin et al., 2010, 2016), and it was 20 m in the present study. The major ions are sulfate > chloride >bicarbonate, and sodium > magnesium. In recent years, the water level of the lake has increased and salinity (as ash content) has decreased to below 14-15 g l^{-1} in the epilimnion and 18-19 g l^{-1} in deeper waters (Rogozin et al., 2010). Zooplankton in the pelagic and open littoral zones are dominated year-round by *Arctodiaptomus salinus* (Copepoda, Calanoida), with the addition of *Brachionus plicatilis* and *Hexarthra spp.* (Rotifera) (Zotina et al., 1999; Zadereev and Tolomeyev, 2007). The major predator in this fishless lake is the amphipod *Gammarus lacustris* in the littoral and the pelagic zones (Tolomeyev et al., 2006; Zadereev et al., 2010).

Our study was conducted on 18-30 June, 2015, at a deep point (water depth 20 m) of the lake, where sediment traps were deployed in the upper part of the hypolimnion. The related hydro-physical recordings were made at ca. 250 m away from the traps. The temperature profile was measured by a thermistor chain consisted of a common logger and 30 digital temperature sensors DS18b20 (Maxim Integrated Products, resolution 0.1°C, absolute accuracy 0.5°C) with a spacing of 0.5 m from 3.5 to 13.5 m and of 1-1.5 m for the other depths. The scanning interval was 30 s. An upward-looking 600 kHz acoustic Doppler current profiler (ADCP, manufactured by Teledyne RDI-Instruments, USA) was deployed at 16 m. The ADCP scanned the water column on 25-30 June in 0.5 m bins at the sampling rate of 2.66 s. The velocity profiles were internally averaged over 120 s. On 13 and 29 June, profiles of temperature and conductivity were taken with YSI-6600 V2 sonde (YSI Inc., USA). Wind speed and direction were measured by a land-based Vantage Pro 2 weather station (Davis Instruments, USA) ~ 0.5 km from the lake at averaged intervals of15 min.

Sediment traps and video recording

Three sediment traps were deployed close to each other at 14 ±1 m for three consecutive days from 18 to 21 June, and for 7 days from 24 to 30 June. The trap exposure time was 24 h, except on 24 June when the exposure time was 2 d (24-26 June) due to a storm on 25 June. Each trap consisted of a pair of cylindrical collectors (Hákanson, 1984). Each collector had the internal diameter of 0.103 m and the internal height of 0.7 m, the height-to-diameter ratio of 6.8 satisfied the requirement to prevent resuspension (Hákanson et al., 1989). Before deploying, the cylinders were filled with water from 14 m depth pre-screened through an80-μm mesh. Each trap was moored to an anchor and a submerged buoy, and marked by a surface float (Fig. 1). Upon trap retrieval, zooplankton samples from the paired collectors were pooled, concentrated on an80-μm mesh and counted for carcasses (Y in Eqs.3 and 4).

To check whether *Gammarus lacustris* could actively penetrate the traps, and whether some resuspension of sediment material occurred during the deployment, one trap collector was equipped

with a video-recorder and a light source (Fig. 1). The digital video recorder Prestige DVR-022 (China) in a waterproof box was externally mounted to the bottom glass window of the cylinder and recorded in upward direction (640×480, 30 fps). The lower part of the cylinder was illuminated by a waterproof LED strip. The light intensity was low enough not to attract 'swimmers', but sufficient for video recording. Power for the video-recorder and LEDs was provided by a waterproof 12 V10 Ah battery case attached to the anchor (Fig. 1). Video data were processed using the ImageJ v.1.46 software. The video was converted to a stack of images. Each image (frame) was subsequently filtered to remove noise and background roughness, so that moving objects were clearly seen. The number of animals per image was automatically registered by the built-in particle analyzer of ImageJ. Five-hour long video recordings during the night and the day were taken on 21 and 26 June, respectively. The field of view was about 100 ml where copepods were easily recognized; gammarids, if present, could be detected at a longer distance.

Water column zooplankton sampling

Zooplankton were collected near the traps daily at around 10-11 a.m. with an open-close Juday net (80 μm mesh and mouth dia. 20 cm) from 15 to 12 m depth to obtain carcass abundance at trap depth(y*), and from 12 m to surface to obtain depth-averaged live and dead abundances above the trap, which were used to calculate weighted means of N_i and y_i for 0-15 m layer (see *Mortality calculations*). Additional stratified net tows were done to obtain vertical distributions of live and dead *A. salinus* at 3-0, 6-3, 9-6, 12-9 and 15-12 m on 21 July (7-8 a.m.), 24 July (9-10 a.m. and 11-12 p.m.) and 28-29 July (11 a.m. and 12 p.m.).

Staining and counting of zooplankton

To distinguish between live and dead zooplankton, samples from the net and sediment traps were stained within an hour after collection with water-soluble aniline blue (Dubovskaya, 2008; Bickel et al., 2009) using a staining device (Gladyshev et al., 2003), and fixed in 10% formalin. Before counting, each sample was acidified according to Bickel et al. (Bickel et al., 2009). In the samples, only the most abundant species, *Arctodiaptomus salinus,* was counted under a microscope for live (unstained) and dead (stained blue) males, females, copepodites V (C5), copepodites I-IV (C1-4) and nauplii. Fragmented carcasses and exuviae were not counted. *Gammarus lacustris,* as potential 'swimmer' and consumer of *A. salinus,* was also counted.

In situ carcass sinking velocity

Daily *in situ* sinking velocities of carcasses (v*) of each developmental stage were calculated according to Eq. 4. The trap input area S (0.0167 m^2) was calculated as sum of mouth area of pair of

collectors. y^*_{av} was calculated as the average of samples taken at the beginning and at the end of the daily trap exposure, or the average of the two samples plus an additional night sample.

Mortality calculations

Specific NPM (m) of *A. salinus* nauplii, C1-4, C5, males and females were calculated for layer 0–15 m using Eqs.16and 17for three periods, 19-21 June (Δt_1), 21-26 (Δt_2) and 24-29 June (Δt_3). Weighted means of abundance of these stages for 0-15 m ($\bar{N}_i$, $\bar{y}_i$ and $\bar{y}_{i+1}$ in Eqs 16, 17) were calculated for each day as $[N_{(0\text{-}12)} \times 12\text{m} + N_{(12\text{-}15)} \times (15\text{-}12\text{m})]/15\text{m}$ or $[N_{(0\text{-}3)}+N_{(3\text{-}6)}+N_{(6\text{-}9)}+N_{(9\text{-}12)}+N_{(12\text{-}15)}]/5$, where $N_{(0\text{-}12)}$, $N_{(12\text{-}15)}$, $N_{(0\text{-}3)}$, $N_{(3\text{-}6)}$, $N_{(6\text{-}9)}$, $N_{(9\text{-}12)}$ and $N_{(12\text{-}15)}$ are abundances in the corresponding layers 0-12 m, 12-15 m, 0-3 m, 3-6 m, 6-9 m and 9-12 m. The means for 24 and 29 June were averaged over day-night data. The specific rate of elimination due to sinking (G) was calculated from Eq. 6 using the water column depth above the traps h = 14 m. Daily sinking velocity (v^*) was time-averaged for Δt_1, Δt_2 and Δt_3.

Steps were taken to minimize potential errors in estimating live and dead *A. salinus* abundances as described in Dubovskaya et al.(2015): (i) traps were exposed for 24±1 h (except 24-26 June, 48 h) to increase accuracy of Y; (ii) two to three replicate traps were exposed simultaneously to increase accuracy of Y by increasing the total value of S and to increase precision of Y; (iii) large volume plankton samples (94-376 L) were collected at trap depth and in the overlying water column to increase accuracy of y^*, $\bar{N}_i$ and $\bar{y}_i$;(iv) sampling at trap depth was done 2–3 times per day to increase precision of y^* and to integrate daily variations (patchiness) of y^*.

Estimation of stratification and turbulence

The background stratification and mixing conditions were estimated from the profiles of density ρ and the coefficient of the vertical turbulent exchange K_Z. Water density as function of time and depth $\rho(z, t)$ was calculated from temperature and salinity following Millero et al.(Millero et al., 1980). The time- and depth-resolved temperatures were taken from the thermistor chain, the salinity profile was obtained from averaging the electric conductivity profiles of four subsequent CTD casts in the vicinity of the thermistor chain. Conductivity was transformed to salinity using the specific formula based on the ion composition of Lake Shira (Rogozin et al., 2010).

The coefficient of vertical turbulent exchange K_Z at depth z was estimated by integrating the vertical density transport from the lake bottom H to z:

$$\int_H^z \frac{\partial \rho}{\partial t} = \int_H^z \frac{\partial}{\partial z} K_Z \frac{\partial \rho}{\partial z} \qquad (18)$$

or

$$\int_H^z \frac{\partial \rho}{\partial t} = \left(K_Z \frac{\partial \rho}{\partial z} \right)_z - \left(K_Z \frac{\partial \rho}{\partial z} \right)_H . \quad (19)$$

Neglecting the vertical density gradient at the lake bottom, the final expression for K_Z is

$$K_Z = -\frac{\int_H^z \frac{\partial \rho}{\partial t}}{\left(\frac{\partial \rho}{\partial z} \right)_z} \quad (20)$$

which is subsequently solved numerically using finite differences for differentiation and trapeze method for integration.

Statistical analysis

Standard deviation (SD), coefficient of variation (CV), standard error (SE), one-way and two-way ANOVA were calculated conventionally using the STATISTICA software, 9.0 (StatSoft Inc., Tulsa, OK, U.S.A.).Only normally distributed variables (after Kolmogorov-Smirnov test for normality) were used for ANOVA. Relative error (%) was calculated as RE = (SE/mean value) × 100.

Results

Environmental conditions, thermal stratification and turbulence

The daily mean wind speed varied from 1.8 to 4.6 m s^{-1}, and the current speed at the sediment trap depth of 14 m was ≤ 4.6 cm s^{-1} (Fig.2A). Daily mean water temperature in the epilimnion (0-6 m) varied slightly from 18.6 to 20.6°C, in the thermocline (6-12 m) increased from 7.7°C on 19th June to 10.7°C on 29th June, and in the upper oxic hypolimnion (12-15 m) increased slightly from 1.4°C on 18-21th June to 1.8°C on 30th June. Temperature at the trap depth varied during the study from 0.6 to 2.8°C with the mean of ca. 2°C (Fig 2 B,C).

Overall, the water column consisted of a shallow epilimnion exposed to wind mixing, a strong thermocline starting at ~6 m depth and a halocline starting at ~9 m depth. The resulting pycnocline occupied the layer of 8-15 m depth with a density difference of ~5 kg m^{-3}across (Fig. 2C). The lower part of the pycnocline, between ~12 m and 15 m, was occupied by a cold oxic hypolimnion with an anoxic monimolimnion beneath. The turbulent mixing, as expressed by K_Z, was characterized by high intensity at the lake surface (Fig. 2D), K_Z up to 10^{-1} m^2 s^{-3}. High turbulence at the surface was apparently produced by wind, in particularly during the storm events on 21-22 June and 24-26 June (Fig. 2A). K_Z quickly decreased with depth to < 10^{-5} m^2 s^{-3} close to the lake bottom, which can be treated as non-turbulent background value when taking into account the accuracy of

the method. A small local maximum of mixing intensity between 14 and 16 m depth (Fig. 2d) was likely the result of internal wave breaking, as indicated by the isotherm oscillations (Fig. 2B).

Vertical distribution of live and dead Arctodiaptomus salinus

Live nauplii and small copepodites (C1-4) were abundant in the epilimnion (0-6 m) with maxima near the surface (0-3 m, Fig. 3). Live males and females occupied the epilimnion and the upper metalimnion (0-9 m) with maximal abundances also in the 0-3 m layer (Fig. 3). Live late copepodites (C5) congregated in the metalimnion (6-12 m) (Fig. 3). Copepodites C5 contained many visible fat droplets in their bodies. Abundances of C5 and adults were substantially lower than that of nauplii and copepodites C1-4, which dominated the population (Fig. 3). The nighttime vertical distribution of all stages was similar to that in the daytime (Fig. 3).

Carcass abundances of all stages were low (Fig. 3). Vertical distribution of carcasses generally followed that of live animals. However, in many cases, the carcass abundance maxima were located below the live copepod abundance maxima. The abundances of both live and dead individuals of all stages, except C5, were lowest in the trap layer (12-15 m) (Fig. 3).

Trap and water column samples

The number of *A. salinus* carcasses accumulated in the traps per day (Y) varied considerably during the study period (Table 1). Kolmogorov–Smirnov test showed a normal data distribution of each stage: $D_{K\text{-}S}$ varied from 0.21 ($p = 0.29$) for females to 0.27 ($p = 0.08$) for C5. Relative errors of Y estimation by 3 traps (2 traps 18-19th, 26-28th June) varied from low (0–14.3% for different stages; Table 1) to high under low carcass abundance (100% for nauplii, 42.9% for C1-4 and for males, 67% for C5 and 60% for females; Table 1). Errors averaged for the whole period for the different stages were rather low, 22-47% (Table 1). Relative errors of estimation of carcass abundance at trap depth (y^*_{av}) also varied widely: 1.2-81.2% for nauplii, 9-61.7% for C1-4, 1.7-76% for C5, 0-55.8% for females and 0-62.5% for males (Table 1), with averaged values of 22-38% (Table 1). y^*_{av} values showed normal distribution: $D_{K\text{-}S}$ ranged from 0.17 ($p = 1.0$) for C5 to 0.25 ($p = 0.63$) for C1-4.

At the trap depth (12-15 m), no individuals of *Gammarus lacustris* were found (Table 2). This species occupied the overlying water column 0-12 m, with maximal abundance at 0-3 and 3-6 m (Table 2). The maximal concentration observed was 29 ind m^{-3}, which occurred the morning after the storm on 25 June. One swimmer of *G. lacustris* per trap was found sporadically, on a total of only 4 occasions(Table 2). The gut of the first swimmer (18-19 June) was empty, the guts of the others, as well as gammarids from the net samples, contained *A. salinus* remains (of males, females,

copepodites, eggs), but it could not be determined whether live or dead *A. salinus* individuals were ingested.

Video recordings confirmed very stable conditions of the water column. Even when the traps were pushed by changing currents around over the line, no resuspension was seen. During the day, the number of *A. salinus* in the field of view did not change (Fig. 4). Slight increase in number could be seen at night before sunrise, but it returned to previous level after two hours (Fig. 4). These changes obviously did not affect the calculations of sinking rates of *A. salinus* carcasses. No *G. lacustris* was seen in any of the video recording, confirming that the amphipod rarely, if ever, entered the traps (Table 2).

Carcass sinking velocity

In situ sinking velocity of *A. salinus* carcasses varied among traps and days (Table 3), and one-way ANOVA indicated significant difference among developmental stages ($F_{4,85} = 8.5$, $P<0.05$). Males and females, which were larger than the other stages, had the highest v^* values, averaging 8.3and 8.5m d^{-1}, respectively (Table 3). Interestingly, copepodites C5 of size similar to adults but containing many fat droplets in their body, which were indicative of diapause, had the lowest averaged sinking velocity at 2.0 m d^{-1}.Two-way ANOVA showed that mean v^* for mortality calculation (Table 3) significantly differed between stages and between time periods: $F_{stages} = 16.7$, $F_{periods} = 17.0$, $P << 0.05$, and their interaction was not significant ($F = 0.4$, $P > 0.05$).

Mortality estimations

Mean abundances of live and dead individuals of *A. salinus* of each developmental stage in the layers 0-15 m ($\bar{N}_i$, $\bar{y}_i$ and $\bar{y}_{i+1}$ in Eqs 16, 17) and 12-15 m (y_i^* in Eq. 17) for calculation of NPM are presented in Table 4. Each $\bar{y}_i$ value was higher than the corresponding y_i^* value with the two exceptions for C5. Consequently, ($\bar{y}_i - y_i^*$) values were rather high and ($y_i^*/\bar{y}_i$) quite low, with two exceptions (Table 4).The coefficient *G*, which represents carcass removal via sinking, ranged from 0.067 to 0.869 d^{-1}, with an average of 0.402 d^{-1} (SD = 0.250 d^{-1}). The coefficient *D*, which represents carcass removal by other processes above trap depth, ranged from 0.021 to 0.823 d^{-1}, with an average of 0.361 d^{-1} (SD = 0.244 d^{-1}) (Table 5). The mortality rates (*m*) calculated with y_i^* were very low, varying from -0.009 to 0.034 d^{-1} (Table 5). Conversely, *m* calculated with $\bar{y}_i$ were higher, at 0.0003-0.103 d^{-1} with one negative value, -0.002 (Table 5). Evidently, the negative values were within range of precision of the method, and therefore should be interpreted as ca. zero mortality. The mortality of all stages was highest at the beginning of the study, between 19 and 21 June (Table 5). This period coincided with the occurrence of maximal percentages of dead individuals of all stages (5.3-10.3 % in 0-15 m, 25.7-83.1 % in 12-15 m), and was followed by a

noticeable decrease in abundances of live animals, most noticeably in nauplii, females and males ($\bar{N}_i$ on 21 and 24 June; Table 4). Minimal mortality of all stages was in the last five-day period, 24-29 June (Table 5). Among all stages, females had the highest mortality (0.103-0.023 d^{-1}) and copepodites C5 the lowest (0.008-0.0003 d^{-1}) (Table 5).

Discussion

Consideration of trap performance

Appropriate choice of sediment trap design and dimensions is crucial for avoiding under-or over-trapping (Buesseler et al., 2007). According to Lau (1979), for a cylindrical trap with an aspect ratio of 6.8, resuspension starts when the trap Reynolds number exceeds 15000. Given our trap dimensions and *in situ* kinematic viscosity of 0.017 cm^2 s^{-1}, such Reynolds number is obtained only at a flow velocity of 24.7 cm s^{-1}, which is much higher than the observed flow velocity at the trap depth (3-4.6 cm s^{-1}). Thus, resuspension from our traps was unlikely. Our video recording also showed no physical disturbance near the trap bottom. Another possible source of error is trap tilt resulting in over-trapping (Gardner, 1985). Our trap design according to Håkanson (1984) kept the cylinders vertically stable irrespective of cable inclination; cable motions and vibrations were further minimized by a subsurface tension buoy (Bloesch and Burns, 1980). Hence, error due to trap tilt would be negligible (Gardner, 1985). Overall, the relative errors of our trap data (22-43%, Table 1) indicate good trap precision (Stanley et al., 2004; Buesseler et al., 2007).

According to our data, there were no marked daily changes in the vertical distribution of dead and live *A. salinus* (Fig. 3). Similarly, Zadereev and Tolomeyev (2007) did not observe any large-scale diel vertical migrations (DVM) of *A. salinus* in the fishless Lake Shira. Therefore, our sampling and calculations were not affected by DVM.

Comparison of $\bar{y}$ and y^*

The population of *A. salinus* was concentrated in the upper 0-9 m, where the largest number of carcasses was also found (Fig. 3). The observed decrease in carcass abundance with depth (Fig. 3) is consistent with the study of Bickel et al. (2009), and suggests that carcass dynamics was affected by processes other than sinking. Both $\bar{y}$ and y^* were estimated with accuracy and precision of the same order of magnitude as those of other field studies (e.g. Dubovskaya et al., 2003). Error (*Er*) of abundance estimation (*A*) by our net sampling method can be calculated as $Er = 2.01A^{0.78}$ (Gladyshev, 1985; Dubovskaya, 1987). This *Er* includes micro-horizontal variability (zooplankton patchiness). For data of $\bar{N}_i$, $\bar{y}$ and y^* (Table 4), *Er* was within a range of 20-109%. *Er* of y^*_{av} in Table 1 (for sinking velocity calculation) varied within 0-81.2 %, comparable to that for *Bosmina* in

Lake Stechlin (1.3-66.2%; Dubovskaya et al., 2015). Although y^* and Y were more variable in a few cases than those reported by Dubovskaya et al. (2015), sampling replications and rather large volumes of zooplankton samples (≥ 94 L) gave a reasonably accurate estimation of $\bar{y}$ and y^*.

Except for two occasions, y^* was in all cases lower than $\bar{y}$, giving low averaged $y^*/\bar{y}$ values of 0.13-0.19 for all stages except C5 (0.77; Table 4). This observation has important ramifications for understanding NPM and carcass dynamics in the lake. Given $\bar{y}>y^*$, it means that many carcasses were removed from the water column before they reached the traps. Under such a condition, the choice of proper formulations is crucial for NPM calculation. When applying Eq. 17 to our data, NPM was-0.009-0.034 d^{-1}; while using Eq. 16 increased NPM estimation to -0.002-0.103 d^{-1} (as explained above, the negative values should be interpreted as zero mortality within the range of precision of the method).The latter values are more realistic, since they follow from the assumption of non-negligible D, which is also supported by $\bar{y}>y^*$ in our observations (see Introduction and Methods). Hence, application of Eq. 17 to sediment trap data would underestimate NPM. Even a small difference in NPM, when propagating through time, could lead to vastly different population growth projections (Elliott and Tang, 2011).

Carcasses in the water column can be removed e.g. by detritivory or microbial degradation. Turbulent mixing can increase the retention time of carcasses in the epilimnion and decrease the ratio $y^*/\bar{y}$. The coefficients G and D were strongly correlated and comparable to each other (linear regression: $D = 0.974\ G - 0.030$; $r^2 = 0.992$), suggesting that both sinking and water column processes were equally important in eliminating carcasses. The coefficient D in our calculations encapsulates the combined effect of different water column processes, but it does not distinguish their relative importance. Nevertheless, below we use independently collected data to examine the roles of these processes in removing zooplankton carcasses above the trap depth.

Possible ingestion of carcasses by Gammarus

The amphipod *Gammarus lacustris* was the main predator in the fishless Lake Shira. Consistent with the data by Zadereev et al. (Zadereev et al.,2010) and Tolomeyev et al. (Tolomeyev et al., 2006), *G. lacustris* occupied the 0-12 m layer, but not below (Table 2). Therefore, *G. lacustris* would not affect *A. salinus* carcass abundance at the trap depth. Rare appearance of *G. lacustris* inside the traps also suggests that this predator had no effect on carcass abundance in the traps or calculation of carcass sinking velocity from trap data.

Previous studies in Lake Shira have shown *G. lacustris* as the top predator of live and dead individuals of *A. salinus* and Rotifera in the epi-and meta-limnion (Yemelyanova et al., 2002; Gubanov, 2009). We found *A. salinus* remains in the guts of *G. lacustris* from the net and trap samples. Although we could not determine the original vital state of the ingested individuals, our

observations at least indicate that the amphipod could potentially ingest *A. salinus* carcasses above the trap depth and contribute to the removal coefficient *D*.

The potential loss of carcasses due to ingestion by *G. lacustris* could be estimated from the daily energy expenditure of the amphipod. An individual of *G. lacustris* with a body length of 10 mm weighs ca. 11.60 mg (Yemelyanova et al., 2002) and has a respiration rate of 4.2 µl O_2 ind^{-1} h^{-1} at the epilimnic mean temperature of 20°C (Sushchenja, 1972). Its daily energy expenditure can be estimated as $R = (0.0042 \times 24 \times 4.86)/0.9 = 0.544$ mg $ind^{-1}day^{-1}$, where 4.86 cal ml^{-1} O_2 is oxycaloric coefficient and 0.9 cal mg^{-1} is caloric content of wet mass (Winberg, 1986).Assuming an assimilation efficiency of 0.8 (Winberg, 1986), the required prey consumption would be 0.680 mg $ind^{-1}d^{-1}$. Given a wet weight of 0.068 mg for adult *Arctodiaptomus* (Balushkina and Winberg, 1979), this is equivalent to a consumption of ~10 carcasses ind^{-1} d^{-1}.The maximal abundance of *G. lacustris* in the 0-12 m layer was 29 ind m^{-3}, which translates to a maximal removal of 290 ind m^{-3} of adult *A. salinus* carcasses. This estimated value is comparable to the averaged difference between $\bar{y}$ and y^* for female and male *A. salines* carcasses (242 and 249 ind m^{-3}, respectively; Table 4). Therefore, ingestion of carcasses by *G. lacustris* within 0-12 m could explain the loss of carcasses.

Turbulence effect and microbial decomposition

Among the nauplii, C1-4 and adults, the average carcass sinking velocity (v^*) increased in accordance with the increase in body size. An interesting exception was C5, which had the lowest carcass sinking velocity and it is likely due to the presence of fat droplets in its body (e.g. Stepanov and Svetlichnyyi, 1981). The presence of fat droplet may allow C5 (both live and dead) to achieve neutral buoyancy and congregate within 6-12 m as observed in our field sampling.

The *in situ* carcass sinking velocities of *A. salinus* (2.0-8.5 m d^{-1}) were in general much lower than those obtained by *in vitro* settling column method. For example, *in vitro* sinking velocity was 35.4±15.6 m $d^{-1}$for *Acartia tonsa* C1-3 carcasses (Elliott et al., 2010), and 112.1±20.3 m d^{-1} for *Eudiaptomus gracilis* adult carcasses (Kirillin et al., 2012). *In vitro* sinking velocity in the absence of any water motion and physical gradients should be regarded as «maximal» (Ploug et al., 2008), or «potential» sinking velocity (Grossart and Simon, 1998). In contrast, *in situ* sinking velocity calculated from Eq.4 represents the average downward velocity of sinking and suspended particles (McDonnell et al., 2010; 2015). Carcasses may achieve positive buoyancy due to microbial decomposition and float upward (Elliott et al., 2010; Kirillin et al., 2012)—a phenomenon known as "anti-rain" of carcasses (Dubovskaya et al., 2015), and not be captured by the traps.

Wind-driven currents and turbulence may also decrease carcass sinking velocities, leading to a lower average v^* and a lower mortality rate that can be accounted for by carcass sinking. During our study, wind speed increased on 21-22 June and on 25-26 June, resulting in high-amplitude

oscillations of the isotherms—indicator of intensified internal wave activity, and a ~3-fold increase in current speeds at the trap depth (Fig.2A). Sinking of carcasses might be slowed down by shear turbulence during these periods. Indeed, on 24-26 June the traps yielded rather low values of carcass sinking velocity, especially trap No. 1 and 2 (Table 3). Minimal sinking velocity of male carcasses was obtained in this period (Table 3). This turbulence effect has been described by others: Dubovskaya et al. (Dubovskaya et al., 2003) showed that the sinking velocities of *Daphnia* and *Cyclops* carcasses (v, m d^{-1}) were negatively correlated with wind speed (u, m s^{-1}) as $v = 3.709u^{-0.984}$. Ivory et al. (Ivory et al., 2014) also found a negative relationship between carcass flux measured by traps (y, mg C $m^{-2}day^{-1}$) and mean current velocity at the trap depth (x, cm s^{-1}): $y = 105.9e^{-0.70x}$.

We suggest that turbulence increases the retention time of carcasses in the upper epilimnion, where they can be removed by ingestion and/or microbial degradation. Based on the measured mean sinking velocities (Table 3), carcasses of nauplii from the surface (z = 0 m) would reach the sediment trap at 14 m in 3.8 days, C1-4 carcasses in 2.7 days, and adult carcasses in1.5 days. During this time, microbial degradation as a temperature-dependent process (Eq. 18 in Kirillin et al., 2012) would decrease the carcass excess density by respectively 0.0223, 0.0210 and 0.0188 g cm^{-3}. Assuming an initial carcass density of 1.045 g cm^{-3} (Elliott et al., 2010), microbial degradation would lower the carcass excess density by 50, 47 and 42%, respectively. Such a substantial loss of excess density would greatly increase carcass retention time and remineralization above the traps.

The estimates of turbulent mixing from the flux-gradient method (Fig.2D) also suggest high mixing rates in the epilimnion, apparently driven by wind. The K_Z values in the upper mixed layer of Lake Shira are up to one order of magnitude higher (10^{-1} m^2 s^{-3}) than those measured previously in the similarly sized but more wind-sheltered Lake Stechlin (10^{-3}-$10^{-2}$$m^2$ s^{-3}, Kirillin et al., 2012). Interestingly, according to the random-walk model of turbulence (Kirillin et al., 2012), this increase of K_Z does not produce any significant increase in carcass retention in the epilimnion. Apparently, isotropic chaotic movements have little effect on carcass sinking. However, the circular water motions produced by surface waves, Langmuir circulations, or convective cells may capture relatively small particles (e.g. zooplankton carcasses) for a longer time and contribute to their mechanical destruction. A reliable quantification of these effects requires *in situ* observation of carcasses movement in surface waters.

The stratification in the brackish Lake Shira is appreciably stronger than in freshwater lakes. For example, the density difference across the Lake Shira pycnoclinewas~5 kg m^{-3}, compared to only ~2 kg m^{-3} in Lake Stechlin and Lake Arend (Kirillin et al., 2012). The strong stratification in Lake Shira could further slowdown carcass sinking and promote their degradation in the water column.

Reality check of non-predatory mortality estimates

The decrease in carcass abundance with depth indicates that a significant amount of carcasses was eliminated from the water column above the traps. However, the processes of carcass elimination are difficult to parameterize due to limited observational information, and the removal term remains poorly constrained. Only a rudimentary approach to this problem was attempted by Frangoulis et al. (Frangoulis et al., 2011), who attributed the decrease in carcass flux with increasing depth to decomposition of the sinking material. Hence, the reliability of the otherwise well-established and robust sedimentation trap method to estimate zooplankton NPM requires a more thorough evaluation.

Incorporation of removal processes in addition to sinking (Eqs. 9 and 16) to derive conservative estimates of NPM produces NPM values of 0.0003–0.103 d^{-1}, which are comparable to the non-predatory mortality rates for zooplankton reported in the literature (<0.01-0.15 d^{-1}; reviewed by Tang and Elliott, 2013). For example, the rich fat content observed in C5 was indicative of diapause, and the estimated *m* for C5 (0.0003-0.008 d^{-1}) was indeed close to the minimal physiological death rate of 0.001-0.05 day^{-1} (Shushkina et al., 2000; Dubovskaya, 2009).Two of the three *m* values for females (0.048-0.023) and males (0.049-0.020), on the other hand, were close to the upper limit of senescence death rate of 0.01-0.05 day^{-1} (Tang et al., 2014). The same range of NPM values was reported by Frangoulis et al. (Frangoulis et al., 2011) for copepods derived from "swimmer-excluding" sediment trap data. The minimal mortality of adult calanoid copepods in survival experiments was also within the range of 0.001-0.031 d^{-1} (Kiørboe et al., 2015).

Furthermore, the temporal variation of NPM values was consistent with *A. salinus* abundance data. For example, the relatively high mortality of all developmental stages (the population average 0.061 d^{-1}; Table 5) at the beginning of the study period (19-21 June) was followed by a decrease in the abundance of live nauplii, C1-4, males and females between 21 and 24 June(Table4). During the following intervals Δt_2 and Δt_3, the NPM value decreased initially to 0.022d^{-1}on average and to 0.007 d^{-1}afterwards, and the concurrent variations in the abundance of all developmental stages were also low, suggesting that the population was close to equilibrium.

Conclusion

Notwithstanding the ignorance of zooplankton carcasses in conventional field sampling, it is now evident that zooplankton can suffer, at times significantly, non-predatory mortality and leave behind carcasses. Sediment trap method has been well developed and widely used for studying sinking fluxes. By using sediment traps to collect sinking zooplankton carcasses *in situ*, it is possible to derive NPM from the trap data, as well as to assess the contribution of zooplankton

carcasses to organic carbon flux. Hence, sediment traps, when augmented by water column sampling, provide an effective means to investigate zooplankton non-predatory mortality and the fate of the carcasses.However, the sediment trap method assumes sinking as the major (sole) process removing carcasses. Accordingly, the accuracy of the method can be compromised when carcasses are removed by other processes in the water column before they reach the traps.

In this study, we began with a detailed mathematical analysis of the problem and derived formulations to account for carcass removal from the water column. We then used an empirical study in Lake Shira to compare and contrast the use of depth-integrated average carcass abundance ($\bar{y}$) and depth-specific carcass abundance (y^*) for calculating NPM of the dominant copepod *A. salinus*, and to examine the different water column processes for removing copepod carcasses. We showed that in Lake Shira where carcass abundance decreased with depth, it is essential to take into account removal of carcasses in addition to sinking when calculating NPM. To a first approximation, it can be done by adopting the mean abundance of carcasses in the water column above traps as a characteristic value for estimation of the NPM from the trap data. We also showed that ingestion by the amphipod *G. lacustris*, along with turbulent mixing and microbial degradation, could account for the estimated removal of carcasses above trap depth.

The observation that y^* was considerably smaller than $\bar{y}_I$ means that a good portion of the zooplankton carcasses was retained in the upper water layer, thereby contributing to epilimnic carbon and nutrient cycling, rather than to the benthic food web in Lake Shira.

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Table 1. Number of *Arctodiaptomus salinus* carcasses accumulated in sediment traps per day (Y, ind d^{-1}) and carcass abundances at trap depth, 12-15 m, average of 2-3 samples taken at the beginning and the end of daily trap exposure (y^*_{av}, ind m^{-3}) in Lake Shira (for calculation of v^*).

Date in June	Carcasses in sedimenttrap, Y					Carcasses at trapdepth (12-15 m), y^*_{av}		
	Trap1	Trap2	Trap3	*CV* (%)	*RE* (%)	Abundance	*CV*(%)	*RE* (%)
				Nauplii				
18-19	nd	5	15	70.7	50	127	nd	nd
19-20	20	14	20	19.25	11.1	167	33.9	24
20-21	41	20	23	40.6	23.4	210	1.7	1.2
24-26	0.5	0.5	1	43.3	25	49	12.9	7.4
26-27	6	1	nd	101	71.4	69	32.8	23.2
27-28	1	0	nd	141.4	100	154	63.4	44.8
28-29	1	0	1	86.6	50	85	140.7	81.2
Mean	-	-	-	-	47.2	116.9	-	36.2
				C1-4				
18-19	nd	5	9	40.4	28.6	64	nd	nd
19-20	9	9	11	12	6.9	83	31.7	22.4
20-21	33	12	33	46.6	26.9	146	43.6	30.8
24-26	3	3	2.5	10.2	5.9	81	15.6	9
26-27	13	12	nd	5.7	4	154	73.5	51.9
27-28	10	4	nd	60.6	42.9	483	72.9	51.6
28-29	7	2	4	58.1	33.5	329	106.9	61.7
Mean	-	-	-	-	22.1	200.8	-	37.6
				C5				
18-19	nd	1	2	47.1	33.3	21	nd	nd
19-20	7	2	4	58.1	33.5	88	107.5	76
20-21	17	4	1	116	67	152	2.3	1.7
24-26	1	0	1.5	91.7	52.9	134	50.7	29.3
26-27	1	4	nd	84.9	60	165	40.8	28.9
27-28	2	7	nd	78.6	55.6	128	11.6	8.2
28-29	1	1	1	0	0	81	72	41.6
Mean	-	-	-	-	42.5	107.5	-	27.4
				Females				
18-19	nd	2	8	84.6	60	21	nd	nd
19-20	13	8	9	26.5	15.3	48	78.9	55.8
20-21	24	8	6	77.9	45	74	0	0
24-26	2	1	3	50	28.9	25	48.5	28
26-27	3	4	nd	20.2	14.3	37	19.1	13.5
27-28	2	5	nd	60.6	42.9	48	16.4	11.6
28-29	1	6	3	75.5	43.6	28	77.4	44.7
Mean	-	-	-	-	36.3	37.8	-	21.9
				Males				
18-19	nd	5	5	0	0	21	nd	nd
19-20	14	8	7	39.2	22.6	56	88.4	62.5
20-21	20	8	11	48	27.7	72	37.3	26.4
24-26	2	0.5	2	57.7	33.3	25	48.5	28
26-27	2	3	nd	28.3	20	27	82.7	58.5
27-28	2	5	nd	60.6	42.9	64	47.9	33.9
28-29	7	8	5	22.9	13.2	42	100	58
Mean	-	-	-	-	26.8	43.6	-	38.2

Table 2. Number of *Gammarus lacustris* in the net column samples (ind. sample^{-1}), at trap depth and inside the traps, Lake Shira, 2015, dash – no samples.

Date in June	Water column					Trap depth	In traps		
	0-3 m	3-6 m	6-9 m	9-12 m	0-12 m	12-15 m	1	2	3
18	-	-	-	-	7	0	-	-	-
19	-	-	-	-	4	0	0	0	1
20	-	-	-	-	-	0	0	1	0
21	2	1	2	0	-	0	1	1	0
24	0	1	0	1	-	0	-	-	-
24 night	1	1	0	0	-	0	-	-	-
26	-	-	-	-	11	0	0	0	0
27	-	-	-	-	8	0	0	0	0
28	-	-	-	-	5	0	0	0	0
29 night	4	4	1	0	-	0	-	-	-
29	1	4	1	1	-	0	0	0	0

Table 3. *In situ* sinking velocity (v*, m d^{-1}) of *Arctodiaptomus salinus* carcasses calculated from Eq. 4 using data from Table 1 for Lake Shira.

Date in June	Trap No	Nauplii	C 1-4	C5	Females	Males
18-19	1	2.36	4.69	2.86	5.72	14.29
	2	7.09	8.44	5.72	22.87	14.29
19-20	1	7.19	6.55	4.80	16.43	15.01
	2	5.03	6.55	1.37	10.11	8.57
	3	7.19	8.00	2.74	11.37	7.50
20-21	1	11.75	13.57	6.74	19.47	16.67
	2	5.73	4.93	1.58	6.49	6.70
	3	6.59	13.57	0.40	4.87	9.17
24-26	1	0.61	2.21	0.45	4.80	4.80
	2	0.61	2.21	0	2.40	1.20
	3	1.22	1.85	0.67	7.20	4.80
26-27	1	5.22	5.07	0.36	4.87	4.53
	2	0.87	4.68	1.46	6.49	6.80
27-28	1	0.39	1.24	0.94	2.53	1.89
	2	0	0.50	3.30	6.32	4.73
28-29	1	0.71	1.28	0.74	2.12	9.93
	2	0	0.36	0.74	12.73	11.35
	3	0.71	0.73	0.74	6.36	7.10
Mean ± SE		3.51±0.82	4.81±0.97	1.98±0.47	8.51±1.40	8.30±1.07
For mortality calculation						
19-21		6.62±0.93	8.29±1.24	3.28±0.80	12.16±2.38	11.52±1.39
21-26		4.42±1.82	6.39±3.58	1.64±1.04	7.54±2.48	7.23±2.17
24-29		1.03±0.48	2.01±0.52	0.94±0.29	5.58±0.99	5.71±1.01

Table 4. Weighted mean abundances (ind m^{-3}) of live and dead *Arctodiaptomus salinus* in 0-15 m water column and at trap depth, 12-15 m, in Lake Shira. For *m* calculations, data on 19, 21, 24, 26, 29 June were used (in bold).

Date in June	0-15 m		12-15 m		$\bar{y}_i - y_i^*$	$y_i^*/\bar{y}_i$
	Live ($\bar{N}_i$)	Dead ($\bar{y}_i$)	Live (N*)	Dead (y_i^*)		
Nauplii						
19	23885	2056	244	127	1929	0.06
20	nd	nd	42	207	nd	nd
21	33158	2202	1672	212	1990	0.10
24	16828	502	202	48	454	0.10
26	12642	397	180	53	344	0.13
27	12040	266	488	85	181	0.32
28	10842	433	467	223	210	0.54
29	7733	151	180	16	135	0.11
Mean±SE	-	-	-	-	749±315	0.19±0.07
C1-4						
19	14928	1706	191	64	1642	0.04
20	nd	nd	42	101	nd	nd
21	28535	2658	1592	191	2467	0.07
24	25520	1132	223	85	1047	0.08
26	24625	1098	382	74	1024	0.07
27	28656	1251	1295	234	1017	0.19
28	45775	2286	1964	732	1554	0.32
29	25615	1080	653	128	952	0.12
Mean±SE	-	-	-	-	1386±209	0.13±0.04
C5						
19	7535	284	106	21	263	0.07
20	nd	nd	446	154	nd	nd
21	3094	276	1672	149	127	0.54
24	3180	138	1290	96	42	0.70
26	5429	119	1932	212	-93	1.78
27	4899	94	1274	117	-23	1.25
28	5432	257	1285	138	119	0.54
29	2953	106	956	53	53	0.50
Mean±SE	-	-	-	-	70±43	0.77±0.21
Females						
19	3839	400	42	21	379	0.05
20	nd	nd	53	74	nd	Nd
21	4602	497	876	74	423	0.15
24	2857	154	181	22	132	0.14
26	2966	261	234	32	229	0.12
27	3640	238	287	42	196	0.18
28	4567	223	276	53	170	0.24
29	2714	182	175	16	166	0.09
Mean±SE	-	-	-	-	242±43	0.14±0.02
Males						
19	9668	334	127	21	313	0.06
20	nd	nd	64	91	nd	Nd
21	13227	737	1274	53	684	0.07
24	9026	161	154	32	129	0.20
26	7197	191	159	11	180	0.06
27	9622	204	340	42	162	0.21
28	12316	176	541	85	91	0.18
29	6982	207	244	21	186	0.10
Mean±SE	-	-	-	-	249±77	0.13±0.03

Table 5. Values of G, D and NPM (d^{-1}) of *Arctodiaptomus salinus* in Lake Shira calculated from Eq.16 and Eq.17.

Daysof June	G	D	NPM	
			FromEq.16(with $\bar{y}_{i)}$	From Eq. 17(with y_i*)
Nauplii				
19-21	0.473	0.443	0.044	0.006
21-26	0.316	0.285	0.010	-0.009
24-29	0.074	0.067	-0.002	-0.004
C1-4				
19-21	0.592	0.570	0.100	0.034
21-26	0.457	0.424	0.032	-0.008
24-29	0.144	0.133	0.006	0.0001
C5				
19-21	0.234	0.217	0.008	0.0001
21-26	0.117	0.054	0.0003	-0.004
24-29	0.067	0.021	0.001	0.00001
Females				
19-21	0.869	0.823	0.103	0.017
21-26	0.538	0.458	0.048	-0.002
24-29	0.399	0.343	0.023	0.005
Males				
19-21	0.823	0.771	0.049	0.023
21-26	0.516	0.479	0.020	-0.006
24-29	0.408	0.327	0.008	0.002
Population mean				
19-21	-	-	0.061±0.018	- (not calculated)
21-26			0.022±0.008	-
24-29			0.007±0.004	-

Table and Figure Legends

Table 1. Number of *Arctodiaptomus salinus* carcasses accumulated in sediment traps per day (Y, ind d^{-1}) and carcass abundances at trap depth, 12-15 m, average of 2-3 samples taken at the beginning and the end of daily trap exposure (y^*_{av}, ind m^{-3}) in Lake Shira (for calculation of v^*).

Table 2. Number of *Gammarus lacustris* in the net column samples (ind. $sample^{-1}$), at trap depth and inside the traps, Lake Shira, 2015, dash – no samples.

Table 3. In situ sinking velocity (v^*, m d^{-1}) of *Arctodiaptomus salinus* carcasses calculated from Eq. 4 using data from Table 1 for Lake Shira.

Table 4.Weighted mean abundances (ind m^{-3}) of live and dead *Arctodiaptomus salinus* in 0-15 m water column and at trap depth, 12-15 m, in Lake Shira. For m calculations, data on 19, 21, 24, 26, 29 June were used (in bold).

Table 5. Values of G, D and NPM (d^{-1}) of *Arctodiaptomus salinus* in Lake Shira calculated from Eq.16 and Eq.17.

Fig. 1. Schematic of the sediment trap with digital video recorder and mooring system.

Fig. 2.(A) Wind speed, and current velocity at 14 m depth; (B) isotherms during the study period; (C) mean vertical profiles of temperature, salinity and density; (D) Vertical profile of the turbulent exchange coefficient K_Z.

Fig. 3. Vertical distribution of live and dead ArctodiaptomussalinusinLake Shira on 21, 24 and 29 June 2015. The shaded panels correspond to the nighttime.

Fig. 4. Number (as 10-min average) of Arctodiaptomussalinusin the sediment trap detected by the video recorder on 21 June (nighttime) and 27 June (daytime). The numbers in the inserts mark animals visible within the field of view.

Effects~~Evaluation~~ of water column processes on the use of sediment traps to measure zooplankton non-predatory mortality~~: of *Arctodiaptomus salinus* in a mathematical and empirical assessment brackish meromictic lake from sediment trap data~~

Olga P. Dubovskaya[1,2*], Aleksandr P. Tolomeev[1], Georgiy Kirillin[3], Zhanna Buseva[4], Kam W. Tang[5], Michail-I. Gladyshev[1,2]

1 Institute of Biophysics of Federal Research Center "Krasnoyarsk Science Center" of Siberian Branch of Russian Academy of Sciences, 50/50 Akademgorodok, Krasnoyarsk, 660036, Russia,

2 Siberian Federal University, 79 Svobodny avenue, Krasnoyarsk, 660041, Russia,

3 Department of Ecohydrology, Leibniz-institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, Berlin, 12587, Germany

4 Practical Center of the National Academy of Sciences of Belarus for Bioresources, 27 Akademicheskaya Street, 220072, Minsk, Belarus

5 Department of Biosciences, Swansea University, SA2 8PP, U.K.

* corresponding author e-mail: dubovskaya@ibp.krasn.ru

Running head: Zooplankton~~Evaluation of~~ non-predatory mortality

Keywords: zooplankton, *Arctodiaptomus salinus*, non-predatory~~non predation~~ mortality, sediment trap, carcasses, stratified lake

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Abstract

Zooplankton populations can at times suffer mass mortality due to non-predatory mortality (NPM) factors, and the resulting carcasses can be captured by sediment traps to estimate NPM rate. This approach assumes sinking to be the primary process in removing carcasses, but in reality carcasses can also be removed by ingestion, turbulent mixing and microbial degradation in the water column. We presented mathematical formulations to calculate NPM from sediment trap data by accounting for carcass removal by processes in addition to sinking, and demonstrated their application in a field study in Lake Shira. Carcass abundance of the major calanoid copepod *Arctodiaptomus salinus* decreased with depth, indicating the effect of carcass removal from the water column. The estimated NPM values were comparable to physiological death rates reported in the literature. We further used independent data to partition carcass removal into detritivory, turbulent mixing and microbial degradation. Estimated ingestion by the amphipod *Gammarus lacustris* could account for the disappearance of copepod carcasses above the traps. Wind-driven currents and turbulence could also extend the carcass exposure time to microbial degradation. Collectively, these water column processes would facilitate the remineralization of carcasses in the water column, and diminish the carcass carbon flux to the benthos.

~~Mortality is one of the principal determinant of population dynamics. However, estimation of this parameter for natural zooplankton *in situ* faces considerable uncertainties. In some periods, declines of zooplankton might be almost completely caused by high non-predatory mortality (NPM). Two variants of *in situ* NPM rate estimation from carcass abundances and sinking velocities was investigated. These variants differ by a single parameter, y_t, carcass abundance above the sediment trap, or y^*, carcass abundance at the trap depth. To compare these two equations, a population of *Arctodiaptomus salinus* in fishless meromictic Shira Lake, which had stratified vertical distribution, was studied. The sediment traps were suspended in an upper hypolimnion, where potential "swimmer" and predator *Gammarus lacustris* was absent. Values of *Arctodiaptomus* NPM, determined by the equation with y_t, 0.001–0.103 d^{-1}, were in good agreement with literature data and the abundance dynamics. NPM values from the equation with y* were too low to be realistic. Thus, the equation with y_t appeared to be more suitable for the mortality estimations of field data. Considerably lower values of y^* compared with y_t mean that zooplankton carcasses in deep stratified lakes contribute to pelagic carbon mineralization and nutrient recycling, rather than to benthic food webs.~~

Introduction

Zooplankton ~~Population dynamics is known to be determined by balance of birth rate and death rate (or total mortality). To predict the~~ population dynamics is determined by two fundamental processes: Birth and death. In ~~of natural zooplankton, the mortality evidently is of the same importance as birth rate. However, in~~ contrast to birth rate, estimation of ~~mortality of zooplankton is known to face considerable uncertainties due to difficulties in measuring~~ *in situ* zooplankton mortality is logistically challenging (Dubovskaya, 2009; Tang and Elliott, 2013; ~~-~~Kimmerer, 2015). Apart from predation, zooplankton can suffer ~~is eliminated by~~ non-predatory mortality (NPM) such as senescence, environmental stresses, food limitation, diseases and parasitism (Tang et al., 2014), and leave behind carcasses. The importance of NPM in constraining zooplankton population growth has been demonstrated theoretically (Gentleman and Head, 2017) and empirically (Elliott and Tang, 2011). It ~~, which~~ can account for on average 25-33% of the total mortality among epi-pelagic marine copepods (Hirst and Kiørboe, 2002; Elliott and Tang, 2011); in some cases, NPM is the main cause of zooplankton population collapse (e.g. Gries and Gude, 1999; Dubovskaya et al., 2003; Wagner et al., 2004).~~2011). In some observations, high NPM was the main determinant for population dynamics (e.g. Gries and Gude, 1999; Dubovskaya et al., 2003; Wagner et al., 2004; Tang and Elliott, 2013). Recently, crucial importance of NPM for a realistic description and prediction of a population dynamics has been demonstrated practically (Elliott and Tang, 2011) and theoretically (Gentlman and Head, 2017). NPM can result from senescence, physical or chemical stresses (including harmful algal blooms), food quantity or quality limitation, diseases and parasites, etc (Tang et al., 2014 and references therein). Non predatory mortality leaves behind intact carcasses, which can be identified by use of special methods, like staining (Tang and Elliott, 2013; Tang et al., 2014).~~

Sediment traps are widely used to collect sinking matter for characterization and to quantify sinking fluxes (Buesseler et al., 2007), and appearance of zooplankton carcasses (distinguishable from swimmers) in sediment traps indicates the role of sinking in removing zooplankton carcasses from the water column (Frangoulis et al., 2011;Dubovskaya et al., 2015). Several sediment trap studies have highlighted the contribution of zooplankton carcasses to the carbon sinking flux (Sampei et al., 2009, 2012; Ivory et al., 2014); sediment trap data also have been used to estimate carcass sinking rates and NPM (Dubovskaya et al., 2015).

In addition to sinking, zooplankton carcasses can be removed by a multitude of water column processes such as microbial decomposition, detritivory and turbulent mixing before the carcasses reach the traps (Dubovskaya, 2008; Elliott et al., 2010; Kirillin et al., 2012).Indeed, a decrease in carcass abundance with depth has been reported (e.g., Bickel et al., 2008). Therefore, proper calculation of NPM requires knowledge of both the mean carcass abundance in the water column

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above the sediment trap ($\bar{y}$) and carcass abundance at sediment trap depth (y^*). By comparing $\bar{y}$ and y^*, we can also gain insights into the relative importance of sinking vs. other removal processes in controlling the fate of zooplankton carcasses. In the simplest terms, we can consider two scenarios: (i) $\bar{y} \leq y^*$ suggests sinking dominates over other processes in removing carcasses from the water column; (ii) $\bar{y} > y^*$ suggests other processes are also important in removing carcasses (see Methods section for details).

Here we use Lake Shira, a fishless brackish meromictic lake in Russia, as a model system to study in situ NPM and carcass dynamics of the dominant species *Arctodiaptomus salinus* (Copepoda: Calanoida). The objectives were to estimate NPM from sediment trap data and investigate the relative importance of sinking vs. other removal processes—encapsulated by the removal coefficient D—in controlling carcass dynamics in the water column. We further attempted to partition D by independently estimating microbial degradation, turbulent resuspension, and detritivory by the dominant invertebrate predators.

~~The amount of zooplankton carcasses in water column is a result, on the one hand, of mortality rate, and on the other hand, of sedimentation and microbial decomposition, which remove these microbial "hotspots" (Tang et al., 2014) from the pelagic zone. Sedimentation is believed to be a faster process than the decomposition, and therefore plays a major role in the elimination of zooplankton carcasses from the water column (Dubovskaya et al., 2003; Dubovskaya, 2008a; Elliott et al., 2010). However, estimates of the sinking velocities of dead zooplankton in natural waters are scarce and equivocal, and their values vary by several orders of magnitude (Tang et al., 2014). Recently, Dubovskaya et al. (Dubovskaya et al., 2015) compared three methods of sinking velocity estimation, applied to carcasses of *Bosmina longirostris* (Crustacea: Cladocera) in Lake Stechlin: 1) *in vitro* settling column method; 2) settling column method corrected for turbulence re-suspension and microbial degradation in lake conditions (model); 3) *in situ* sediment trap data. *In situ* sinking velocities (mean 1.7 m d^{-1}) were about two orders of magnitude lower than *in vitro* estimations (134 m d^{-1}) and model simulations (75 m d^{-1}). Noteworthy, the latter two methods produced unrealistically high NPM rates of 0.58–1.04 d^{-1}, whereas the sediment trap velocity yielded the mortality rate estimate of 0.015 d^{-1}, which was consistent with concurrent population abundance data (Dubovskaya et al., 2015).~~

~~A direct method of measuring *in situ* NPM was proposed by Gladyshev and Gubanov (Gladyshev and Gubanov, 1996). The method is based on temporal carcass dynamics in a studying water column and assumption that carcass sinking is the principal component of their elimination from the water column, and velocity of their sinking is measured using sediment traps beneath (Equation 6 in Methods). It was applied to a shallow (0–2 m), mixing layer of a small reservoir with nearly homogenous vertical distribution of *Daphnia* and cyclopoids carcasses and live individuals~~

~~(Gladyshev et al., 2003; Dubovskaya et al., 2003; 2008b). The second variant of this method (Equation 8 in Methods) is first presented in (Dubovskaya et al., 2015), where NPM estimation based on direct measurement of carcass flux from the whole water column by the sediment traps beneath. The only difference between these two variant of NPM calculation consists in using mean carcass abundance in water column above the trap exposure depth (y_t) in the first case and abundance of carcasses at the trap depth (y^*) in the second case. If $y_t \approx y^*$, both variants will give the same NPM values. A population of *Bosmina longirostris* in deep Lake Stechlin congregated in the metalimnion just above the trap depth, 12 m, satisfying the condition $y_t \approx y^*$ (Dubovskaya et al., 2015). If vertical distribution of a population is stratified with a peak in the upper epilimnion, and trap depth is in the meta- or hypolimnion, than y_t may be much higher than y^*, and the corresponding NPM values will have the same difference.~~

~~The goals of the present study are: (i) to estimate *in situ* NPM dynamics of *Arctodiaptomus salinus* (Copepoda: Calanoida) in a brackish meromictic lake, where the population has pronounced vertically stratified distribution, and strongly affected by the physical environment; (ii) to test and refine the approaches to the NPM estimation from the sediment trap data basing on comparison of the two variants of NPM estimation in conditions of strong density stratification, when the sediment traps are separated from the zooplankton-populated epilimnion by a strong pycnocline.~~

Methods

Non-predatory mortality estimation

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In situ NPM estimations are based on the equation of ~~the~~ vertical transport with a source term in the following form:

$$\frac{\partial y}{\partial t} = mN - \frac{\partial F}{\partial z}, \qquad (1)$$

where m (d^{-1}) is the specific non-predatory~~non-predation~~ mortality, F is the vertical flux of carcasses, N and y are abundances of live individuals and carcasses (ind m^{-3}), respectively. Integration of this equation over the layer $0 < z < h$ above the sediment trap, under the assumption of zero flux of the carcasses across the air-water boundary $F(0) = 0$, yields:

$$\frac{\partial \overline{y}}{\partial t} + \frac{F^*}{h} = \overline{mN}, \qquad (2)$$

where the overbar means averaging over the water column $0 < z < h$; the vertical flux F^* of carcasses at the trap exposure depth h (ind m^{-2} d^{-1}) is directly measured by sediment traps as

$$F^* \equiv v^* y^* = \frac{Y}{S}, \quad (3)$$

and

$$v^* = Y/(Sy^*). \quad (4)$$

Here, Y is number of carcasses accumulated in a sediment trap per day (ind d^{-1}), S is the input area of the trap (m^2), v^* (m d^{-1}) and y^* (ind m^{-3}) are the sinking velocity of carcasses and the concentration of the carcasses at trap exposure depth (i.e. outside the trap), respectively. The final expression ~~for~~ of the non-predatory specific mortality m becomes

$$m = \frac{1}{\bar{N}}\frac{\partial \bar{y}}{\partial t} + \frac{v^* y^*}{\bar{N}h}, \quad (5)$$

subject to subsequent integration with respect to time based on discrete series of measurements on y^* and v^*. Here,

$$G = \frac{v^*}{h} \quad (6)$$

is the specific rate of elimination of carcasses from the water column via sinking. In order to explore the application of Eq. 1and Eq. 5 to estimate NPM, we consider a simple case of depth-constant sinking velocity v. Then, Eq. 1 becomes

$$\frac{\partial y}{\partial t} = mN - v\frac{\partial y}{\partial z}, \quad (7)$$

Assuming further that the live zooplankton are homogeneously distributed throughout the water column (N=constant), and the situation is close to steady state ($\partial y/\partial t \approx 0$), Eq. 1 is solved as

$$y = (mN/v^*)z + y_0, \quad (8)$$

i.e. abundance of carcasses y should increase linearly with depth unless they are removed before reaching the trap. This equation however does not take into account various processes other than sinking, such as turbulence, degradation and detritivory, in removing carcasses from the water column. The combined effect of these processes can be represented by adding a first-order removal rate with a coefficient D to Eq. 1:

$$\frac{\partial y}{\partial t} = mN - v\frac{\partial y}{\partial z} - Dy, \quad (9)$$

In contrast to Eq. 8, solution to Eq. 9 yields exponentially decaying carcass abundance y with depth. To explore its effect on m, we assume the instantaneous carcass abundance is proportional to the abundance of live zooplankton, $y = \delta N$. The analytical solution to Eq. 9 under the same assumptions N = constant and $\partial y/\partial t \approx 0$ is

$$y(z) = y_0 \exp\left(\frac{m - D\delta}{\delta v} z\right), \quad (10)$$

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and the solution with respect to m, analogous to Eq. 5 can be written as

$$m = \frac{1}{\bar{N}}\frac{\partial \bar{y}}{\partial t} + \frac{1}{\bar{N}}\left(D\bar{y} + Gy^*\right) \quad (11)$$

Thus, the mortality rate m_{trap} calculated from sediment trap data is reduced by relative loss rate, as compared with the real mortality *in situ*:

$$m_{trap} = m - D\frac{\bar{y}}{\bar{N}}. \quad (12)$$

Hence, at high removal rate D, carcass abundance at trap depth (y^*) approaches zero, and estimations of mortality from Eq. 5 become unreliable. Its alternative, Eq. 11 requires empirical measurement of D by extensive sampling and analysis of the plankton communities, which is logistically challenging to do in parallel to *in situ* trap measurements. A practical alternative is by adopting the integral sample of carcasses abundance over the entire water column as an approximate of their abundance at the trap deployment depth, i.e. $\bar{y} \approx y^*$, which turns Eq. 5 to:

$$m = \frac{1}{\bar{N}}\left(\frac{\partial \bar{y}}{\partial t} + G\bar{y}\right) \quad (13)$$

This formulation was used for NPM estimations by ~~Two slightly different variants to discretization of Eq. 5 are used.~~ Gladyshev and Gubanov (1996) (~~(Gladyshev and Gubanov, 1996;~~ see also Gladyshev et al., 2003). ~~proposed the following variant:~~

~~$$m_i = \frac{\Delta y}{\Delta t_i \cdot N_i} + G_i \cdot \frac{y_i}{N_i}$$~~

By comparing Eq. 13 and Eq. 5; i.e. replacing y^* with $\bar{y}$, we can estimate the variance in m caused by elimination of carcasses above the trap depth. For example, introducing $\gamma = (D - m/\delta)/v$, one can show that $\bar{y}/y^* \to 1$ at $\gamma h \to 0$, and $\bar{y}/y^* \to \infty$ at $\gamma h \to \infty$, where h, as before, is the depth of the trap exposition. Hence, Eqs.5 and 13 are interchangeable if the traps are positioned close to the depth of the maximum abundance of zooplankton (Dubovskaya et al., 2015), and the error becomes higher with deeper exposition of traps. An intermediate case $\gamma h \approx 1$ yields $\bar{y}/y^* \approx (e - 1) \approx 1.71$, i.e. Eq. 13 would in typical configurations slightly overestimate the mortality rate, but the overestimation is within the range of method accuracy. Eq. 13 becomes equivalent to Eq. 11 if

$$D = G\left(1 - \frac{y^*}{\bar{y}}\right). \quad (14)$$

Hence, *in situ* mortality rates as produced by Eq.13 imply a depth- and time-constant elimination of carcasses at the rate given by Eq. 14. At small y*, Eq. 14 suggests that the elimination of carcasses above the trap is nearly equal in magnitude to the removal of carcasses due to sinking:

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$D \approx G$. (15)

For estimation of the NPM from discrete sampling, a finite difference equivalent of Eq. 13 is used:

$$m_i = \frac{\Delta \overline{y}}{\Delta t \cdot \overline{N}_i} + G_i \cdot \frac{\overline{y}_i}{\overline{N}_i} \quad (16)$$

Where (6)

where m_i (d^{-1}) is the specific NPM at the time t_i (day), $\Delta t_i = t_{i+1} - t_i$, is the period between two sampling events i, $\overline{y}_i$ is the mean abundance of carcasses (ind.·m^{-3}) in water column above the layer of trap exposure at t_i in the water column above the trap, $\Delta \overline{y} = \overline{y}_{i+1} - \overline{y}_i$, $\overline{N}_i$, $\Delta y = y_{i+1} - y_i$, N_i is abundance of live individuals (ind.·m^{-3}) in the water column above the trap. Eq. 5 becomes: trap, and G_i is the specific rate of elimination of carcasses from the water column based on their sinking; $G_i = v^*/h = Y/(S y^* h)$ (7).

The second variant is used by Dubovskaya et al. (Dubovskaya et al., 2015):

$$m_i = \frac{\Delta y}{\Delta t_i \cdot N_i} + G_i \cdot \frac{y^*}{N_i} \quad (17).$$

(8).

The difference between Eq.1 Equation 6 and Eq. 17 is Equation 8 consists in using $\overline{y}$ vs. y^* y_i or y^* in the last term. In the following we applied both Eq. 16 and Eq. 17 to estimate zooplankton NPM in Lake Shira, and to evaluate the relative importance of D vs. G.

Study site

Lake Shira (54.499°N, 90.204° E), situated a brackish meromictic enclosed lake in Russia (South Siberia, the steppe area of Khakassia Republic at, 354 m above sea level, level), has been intensively studied for the last 2 decades (Zotina et al., 1999; Yemelyanova et al., 2002; Rogozin et al., 2010, 2016; see also special issues of Aquatic ecology 2002, 36 (2) and 2010, 44 (3)). The lake area is 35.9 km^2, the maximum depth is 24 m. The depth of the upper boundary of the anoxic monimolimnion with hydrogen sulfide varies seasonally and annually between 11 and 16 m (Rogozin et al., 2010, 2016), and it in summer 2015, this depth was 20 m in the present study. The major ions are sulfate > chloride >bicarbonate, and sodium > magnesium. In recent During last years, the water level of the lake has increased and salinity (as ash content) has decreased to below 14-15 g l^{-1} in the epilimnion and 18-19 g l^{-1} in deeper waters (Rogozin et al., 2010). Zooplankton in the pelagic and open littoral zones are dominated year-round by consist of *Arctodiaptomus salinus* (Copepoda, Calanoida), with the addition of *Brachionus plicatilis* and *Hexarthra spp.* (Rotifera), the first one being the only year-round dominant zooplankton species (Zotina et al., 1999; Zadereev and Tolomeyev, 2007). The major predator top consumer in this fishless lake is the amphipod

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Gammarus lacustris inhabiting the littoral andas well as the pelagic zones (Tolomeyev (Tolomeev et al., 2006; Zadereev et al., 2010).

Our study was conductedcarried out on 18-30 June, 2015, at a deep point (water depth 20 m) of the lake, where three sediment traps were deployedsuspended close to each other at depth 14 ± 1 m from the lake surface in the upper part of the hypolimnion. The related hydro-physical recordings were made at ca.a distance about 250 m away from the exposed traps. The temperature profile was measured bydata for the study period were obtained with a thermistor chain consisted of a common (one) logger and 30 digital temperature sensors DS18b20 (Maxim Integrated Products, resolution 0.1°C, absolute accuracy 0.5°C) with a spacing of 0.5 m from 3.5 to 13.5 m and of 1-1.5 m for the other depths. The scanning interval was 30 s. An upward-lookingA 600 kHz acoustic Doppler current profiler (ADCP, manufactured by Teledyne RDI-Instruments, USA) was deployed upward looking at the water depth of 16 m. The ADCP scanned the water column on 25-30 June in 0.5 m bins at the sampling rate of 2.66 s. The velocity profiles were internally averaged over 120 s. On 13 and 29 June, profiles of temperature and conductivity were taken with YSI-6600 V2 sonde (YSI Inc.,Incorporated, USA). Wind speed and direction were measured byfrom a land-based Vantage Pro 2 weather station (Davis Instruments, USA) ~ 0.5 km from the lake at averaged intervals ofas 15 min. averages.

Sediment traps and video recording

Three sediment traps were deployed close to each other at 14 ±1 m for three consecutive days from 18 to 21 June, and for 7 days from 24 to 30 June. The trap exposure time was 24 h,hours, except on 24 June when the exposure time was 2 days (24-26 June) due to a storm on 25 June. Each trap of type of Hákanson (Hákanson, 1984) consisted of a pair of cylindrical collectors (Hákanson, 1984). Each collector had the internal diameter of 0.103 m and the internal height of 0.7 m, the height-to-diameter ratio of(H/D = 6.8 satisfied) met the requirementrecommended value to prevent resuspension (Hákanson et al., 1989). Before deploying, the cylinders were filled with water from 14 m depth pre-screened through an80–80 μm mesh. Each trap was moored to using an anchoring weight and a stretching submerged buoy, and markedsupplied by a marking surface float (Fig. 1). Upon trapAfter traps retrieval, zooplankton samples from the paired collectors were pooled, concentrated on an80–80 μm mesh and counted for carcasses (processed to obtain values of *Y* in Eqs. 3-4 and 4). 7.

To check whether the 'swimmers', *Gammarus lacustris*, could actively penetrate the traps, and whether some resuspension of sediment material occurred during the deployment, one trap collector was equipped with a video-recorder and a light source (Fig. 1). The digital video recorder Prestige DVR-022 (China) inwith a waterproof box was externally mounted toat the bottom glass window of

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the cylinder and ~~. Video (640×480, 30 fps) was~~ recorded in upward direction (640×480, 30 fps) ~~through the bottom glass window. The objective was manually focused at a distance of 15 cm with the narrow grip of 1.3 cm.~~ The lower part of the cylinder was illuminated by~~with~~ a waterproof LED strip. The light ~~tape to support the recording conditions. The~~ intensity ~~of light~~ was low enough not to attract 'swimmers', ~~outside the trap,~~ but sufficient~~still high~~ for video recording ~~acquisition.~~ Power for~~supply of~~ the video-recorder and LEDs was provided by a waterproof 12 V10 Ah battery ~~capacity placed in a waterproof~~ case attached ~~, which was lowered together with an anchor~~ to the anchor ~~lake bottom~~ (Fig. 1). Video ~~-~~data were processed using the ImageJ v.1.46 software. The video~~recorded movie~~ was converted to a stack of images. Each image (frame) was subsequently filtered to remove~~from~~ noise and background roughness, so that ~~the~~ moving objects were clearly seen. The number of animals per image was automatically registered by the built-in~~determined using build-in~~ particle~~Particle~~ analyzer of ImageJ. ~~ImageJ, with subsequent converting of the frames sequence into the time series of animal's amount.~~ Five-hour long video recordings during the night and the day ~~time~~ were taken~~performed~~ on 21 and 26 June, respectively. The field~~volume~~ of view was about 100 ml where ~~the~~ copepods were easily recognized~~distinguished; however,~~ gammarids, if present, could be detected at a longer distance.

Water column zooplankton sampling~~s~~

Zooplankton were ~~was~~ collected near the traps daily at around 10-11 a.m. with an open-close~~by hauling a closing~~ Juday net (80 µm mesh and mouth dia. 20 cm) ~~(i)~~ from 15 ~~m~~ to 12 m depth~~,~~ to obtain carcass abundance~~y* value~~ at trap depth(y^*)~~depth;~~ and ~~(ii)~~ from 12 m to surface~~,~~ to obtain depth-averaged live and dead abundances ~~N_i, y_i~~ above the trap, which were used to calculate weighted means of N_j and y_j for 0-15 m layer (see *Mortality calculations*). Additional stratified net tows were done~~trap. In addition,~~ to obtain ~~data about~~ vertical distributions of live and dead *A. salinus*~~Arctodiaptomus~~ at ~~day and night the net samples from~~ 3-0, 6-3, 9-6, 12-9 and 15-12 m on~~were taken~~ 21 July (7-8 a.m.), 24 July (9-10 a.m. and 11-12 p.m.) and 28-29 July (11 a.m. and 12 p.m.).

Staining and counting of zooplankton

To distinguish between live and dead zooplankton, samples from the net and sediment traps were stained within an hour after collection with water-soluble aniline blue (Dubovskaya, 2008~~;2008a;~~ Bickel et al., 2009) using a staining device (Gladyshev et al., 2003), and fixed in 10% formalin. Before counting, each sample was acidified according to Bickel et al. (Bickel et al., 2009). In the samples, only the most abundant species~~, of zooplankton,~~ *Arctodiaptomus salinus,* was counted under a microscope for~~:~~ live (unstained) and dead (stained blue) males, females,

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copepodites V (C5), copepodites I-IV (C1-4) and, nauplii. FragmentedInjured carcasses and exuviaeempty exoskeletons were not counted. *Gammarus lacustris,* as potential 'swimmer' and consumer of *A. salinus,Arctodiaptomus,* was also counted.

In situ carcass sinking velocity

Daily *in situ* sinking velocities of carcasses (v^*) of each developmental stage were calculated according to Eq. 4. The trap input area S (0.0167 m^2) was calculated as sum of mouth area of pair of collectors. y^*_{av} was calculated as the average of samples taken at the beginning and at the end of the daily trap exposure, or the average of the two three samples plus an, these two and additional night sample.one.

Mortality calculations

Specific NPM (m) of *A. salinusArctodiaptomus* nauplii, C1-4, C5, males and females were calculated for layer 0–15 m using Eqs.16and 17 6 and 8 for three periods, 19-21 June (Δt_1), 21-26 (Δt_2) and 24-29 June (Δt_3). Weighted means of abundance of these stages for 0-15 m ($\overline{N}_i$, $\overline{y}_i$ N_i, y_i and $\overline{y}_{i+1}$ y_{i+1} in Eqs 16, 17)6, 8) were calculated for each day as [$N_{(0\text{-}12)}$ × 12m + $N_{(12\text{-}15)}$ × (15-12m)]/15m or [$N_{(0\text{-}3)}$+$N_{(3\text{-}6)}$+$N_{(6\text{-}9)}$+$N_{(9\text{-}12)}$+$N_{(12\text{-}15)}$]/5, where $N_{(0\text{-}12)}$, $N_{(12\text{-}15)}$, $N_{(0\text{-}3)}$, $N_{(3\text{-}6)}$, $N_{(6\text{-}9)}$, $N_{(9\text{-}12)}$ and $N_{(12\text{-}15)}$ are abundances in the corresponding layers 0-12 m, 12-15 m, 0-3 m, 3-6 m, 6-9 m and 9-12 m. The means for 24 and 29 June were averaged over day-night data. The specific rate of elimination due to sinking (G) was calculated from Eq. 67 using the water column depth above the traps h = 14 m. Daily sinking velocity (v^*) was time-averaged for Δt_1, Δt_2 and Δt_3.

Steps were taken to minimize potential errors in estimating estimation of live and dead *A. salinusArctodiaptomus* abundances as described in (Dubovskaya et al.(al., 2015): (i)1) traps were exposed for 24±1 h (except 24-26 June, 48 h) to increase accuracy of Y; (ii)2) two to three replicate traps were exposed simultaneously to increase accuracy of Y by increasing the total value of S and to increase precision of Y; (iii)3) large volume plankton samples (94-376 L) were collected at trap depth and in the overlying waterabove column to increase accuracy of y^*, $\overline{N}_i$ and $\overline{y}_i$;(iv) N_i, y_i; 4) sampling at trap depth was done 2–3 times per day to increase precision of y^* and to integrate daily variations (patchiness) of y^*.

Estimation of stratification and turbulence

The background stratification and mixing conditions were estimated from the profiles of density ρ and the coefficient of the vertical turbulent exchange K_Z. Water density as function of time and depth $\rho(z, t)$ was calculated from temperature and salinity following (Millero et al.(Millero et

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al., 1980). The time- and depth-resolved temperatures were taken~~adopted~~ from the thermistor chain, the salinity profile was obtained from averaging the electric conductivity profiles of four subsequent CTD casts in the vicinity of the thermistor chain. Conductivity was transformed to salinity using the specific formula based on the ion composition of Lake Shira (Rogozin et al., 2010).

~~The~~ The coefficient of ~~the~~ vertical turbulent exchange K_Z at ~~every~~ depth z was estimated by integrating~~integration of the equation of~~ the vertical density transport from the lake bottom H to z:

~~:~~

$$\int_H^z \frac{\partial \rho}{\partial t} = \int_H^z \frac{\partial}{\partial z} K_Z \frac{\partial \rho}{\partial z} \quad (18)$$

~~(9)~~

or

$$\int_H^z \frac{\partial \rho}{\partial t} = \left(K_Z \frac{\partial \rho}{\partial z} \right)_z - \left(K_Z \frac{\partial \rho}{\partial z} \right)_H . \quad (19)$$ ~~(10).~~

Neglecting the vertical density gradient at the lake bottom, the final expression for K_Z is

$$K_Z = -\frac{\int_H^z \frac{\partial \rho}{\partial t}}{\left(\frac{\partial \rho}{\partial z} \right)_z} \quad (20)$$ ~~(11)~~

which is subsequently solved numerically using finite differences for differentiation and trapeze method for integration.

Statistical analysis

Standard deviation (SD), coefficient of variation (CV), standard error (SE), one-way and two-way ANOVA were calculated conventionally using the STATISTICA software, 9.0 (StatSoft Inc., Tulsa, OK, U.S.A.). ~~Only~~ normally distributed variables (after Kolmogorov-Smirnov test for normality) were used for ANOVA.~~ANOVAs. For data with non-normal distribution the non-parametric Kruskal-Wallis test was used.~~ Relative error (%) was calculated as RE = (SE/mean value) × 100.

Results

Environmental conditions, thermal stratification and turbulence

~~The weather varied during the study (18-30 June 2015) and during a day from calm to windy up to storm (21, 25 June, Fig. 2).~~ The daily mean wind speed varied from 1.8 to 4.6 m s^{-1}, and the current speed at the sediment trap depth of 14 m~~,~~ was ≤ 4.6 cm s^{-1} (Fig.2A). Daily mean water temperature in the epilimnion (0-6 m) varied slightly~~varied~~ from 18.6 to 20.6°C, in the thermocline (6-12 m) increased from 7.7°C on 19th June to 10.7°C on 29th June, and in the upper oxic

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hypolimnion (12-15 m) ~~slightly~~ increased slightly from 1.4°C on 18-21th June to 1.8°C on 30th June. Temperature at the trap depth varied during the study from 0.6 ~~°C~~ to 2.8-°C with the mean of ca.~~about~~ 2-°C (Fig 2 B,C).

Overall, the water column consisted of a shallow epilimnion exposed to wind mixing, a strong thermocline starting at ~6 m depth and a halocline starting at ~9 m depth. The resulting pycnocline occupied the layer of 8-15 m depth with a density difference ~~across it~~ of ~5 kg m^{-3} across (Fig. 2C). The lower part of the pycnocline, between ~12 m and 15 m, was occupied by a cold oxic hypolimnion with an anoxic monimolimnion beneath. The turbulent mixing, as expressed by K_Z, was characterized by high intensity at the lake surface (Fig. 2D), K_Z up to 10^{-1} m^2 s^{-3}. High turbulence at the surface was apparently produced by wind, in particularly~~particular,~~ during the storm events on 21-22 June and 24-26 June (Fig. 2A). K_Z quickly decreased~~decreases~~ with depth to $< 10^{-5}$ m^2 s^{-3} close to the lake bottom, which can be treated~~assumed~~ as non-turbulent background value when~~,~~ taking into account the accuracy of the method. A small local maximum of mixing intensity between 14 and 16 m depth (Fig. 2d) was likely the~~is most probably a~~ result of internal wave breaking, as indicated by~~observed in~~ the isotherm oscillations (Fig. 2B).

Vertical distribution of live and dead Arctodiaptomus salinus

Live nauplii and small copepodites (C-1-4) were abundant in the epilimnion (0-6 m) with maxima~~reaching maximum~~ near the surface (0-3 m, Fig. 3). Live males and females occupied the epilimnion and the upper metalimnion (0-9 m) with maximal abundances also in the ~~surface layer~~ 0-3 m layer (Fig. 3). Live late~~oldest~~ copepodites (C5) congregated in the metalimnion (6-12 m) ~~with more or less pronounced peak in 9-12 or 6-9 m~~ (Fig. 3). Copepodites C5 contained many visible fat droplets~~drops~~ in their bodies. Abundances~~They may be in state of "quiescence" (Jiménez-Melero et al., 2013). Abundance~~ of C5 and adults were~~was~~ substantially lower than that of nauplii and copepodites C1-4, which dominated ~~in~~ the population (Fig. 3). The nighttime~~nocturnal~~ vertical distribution of all stages was similar to that in the daytime~~diurnal one~~ (Fig. 3).

Carcass abundances~~ Abundance of carcasses~~ of all stages were~~was~~ low (Fig. 3). Vertical distribution of carcasses generally followed that of live animals. However, in many cases, the ~~maximum of~~ carcass abundance maxima were ~~was~~ located below the~~in the layer underlying the layer of the maximum of~~ live copepod abundance maxima.~~individuals (Fig. 3).~~ The abundances of both live and dead individuals of all stages, except ~~but~~ C5, were ~~the~~ lowest in the trap layer (12-15 m) (Fig. 3).~~ Kruskal-Wallis test for live C1-4 and dead nauplii and one-way ANOVA for the other stages revealed abundance differences between the layers were significant ($P < 0.05$, $df_1 = 4$, $df_2 = 20$) except one stage, dead males ($P>0.05$).~~

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Trap and water column samples

The number~~Number~~ of *A. salinus*~~Arctodiaptomus~~ carcasses accumulated in the traps per day (Y) varied considerably during the study period (Table 1). Kolmogorov–Smirnov test showed a normal data distribution of each stage~~: data:~~ $D_{K\text{-}S}$ varied from 0.21 ($p = 0.29$) for females to 0.27 ($p = 0.08$) for C5. Relative errors of Y estimation by 3 traps (2 traps 18-19th, 26-28th June) varied from low (0–14.3% for different stages; Table 1) to high under low carcass abundance (100% for nauplii, 42.9% for C1-4 and for males, 67% for C5 and 60% for females;~~females,~~ Table 1). Errors~~1),~~ averaged for the whole period for the different stages ~~stage errors~~ were rather low,~~in limits~~ 22-47%~~22-43%~~ (Table 1). Relative errors of estimation of carcass abundance at trap depth (y^*_{av}) also varied widely:~~within the wide limits:~~ 1.2-81.2% for nauplii, 9-61.7% for C1-4, 1.7-76% for C5, 0-55.8% for females and 0-62.5% for males (Table 1), with ~~range of~~ averaged values of 22-38% (Table 1). y^*_{av} values showed normal distribution: $D_{K\text{-}S}$ ranged from 0.17 ($p = 1.0$) for C5 to 0.25 ($p = 0.63$) for C1-4.

At the trap depth (12-15 m), no individuals of *Gammarus lacustris* were~~had been~~ found (Table 2). This species occupied the overlying water column 0-12 m, with maximal abundance at~~in the layers~~ 0-3 and 3-6 m (Table 2). The maximal concentration observed~~numerical peak in the whole 0-12 m column~~ was ~~11 ind sample^{-1}, which corresponded to~~ 29 ind m^{-3}, which ~~and that peak~~ occurred the morning after the storm on ~~of~~ 25 June.

One swimmer of *G. lacustris* per trap was found sporadically, on a~~in~~ total of only 4 occasions~~occurrences~~ (Table 2). The gut of the first swimmer (18-19 June) was empty, the guts of the others, as well as gammarids from the net samples, contained *A. salinus*~~Arctodiaptomus~~ remains (of males, females, copepodites, eggs), but it could~~as well as guts of *Gammarus* from the lake samples. It is~~ not be determined whether ~~known, a~~live or dead *A. salinus*~~Arctodiaptomus~~ individuals were ingested.

Video~~In our video~~ recordings confirmed~~, we watched~~ very stable conditions of the water column. Even when the traps were pushed by changing currents~~turn~~ around over the line~~, driven by changing of the direction of current flows,~~ no resuspension was seen. During the day, the number of *A. salinus*~~Arctodiaptomus~~ in the ~~camera~~ field of view did not change (Fig. 4). Slight increase in ~~of the~~ number could be seen at~~found in the~~ night ~~data~~ before ~~the~~ sunrise, but it returned to previous level after two hours (Fig. 4). These changes obviously did not affect the calculations of sinking rates of *A. salinus* carcasses. No *G. lacustris* was~~dead *Arctodiaptomus*. None of *Gammarus* individuals could be~~ seen in any of the video recording, confirming~~frames assuming~~ that the amphipod rarely, if ever,~~this 'swimmer'~~ entered the traps~~, it happened rarely~~ (Table 2).

Carcass sinking velocity

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In situ sinking velocity of *A.~~Arctodiaptomus~~ salinus* carcasses ~~of each stage~~ varied among traps and days (Table 3), ~~however, the data were normally distributed,~~ and one-way ANOVA indicated significant difference among developmental stages ($F_{4,85}$ = 8.5,~~11.1,~~ P<0.05). Males ~~between stages. The largest in size males~~ and females, which were larger than the other stages, had the highest ~~among the 5 stages~~ v* values, averaging 8.3and 8.5m d^{-1}, respectively (Table ~~on average 9.~~3). Interestingly, ~~and 8.9 m d^{-1} (Table 3), the lowest among the 5 stages sinking velocity, on average 2.0 m d^{-1}, was obtained for the oldest~~ copepodites C5 of size similar~~which were close~~ to adults ~~in size~~ but containing~~contained~~ many fat droplets~~drops~~ in their body, which were indicative~~body. The mean values were significantly different for pairs~~ of diapause, had the lowest averaged sinking velocity at 2.0 m d^{-1}.~~nauplii and males or nauplii and females and pairs of C1-4 and males or C1-4 and females, as well as for pairs of C5 and females or C5 and males, and for C5 and C1-4 (Table 3).~~ Two-way ANOVA showed~~revealed~~ that mean~~particular~~ v*~~ means~~ for mortality calculation (Table 3) significantly differed between ~~the~~ stages and between ~~the~~ time periods: F_{stages} = 16.7,~~17.8,~~ $F_{periods}$ = 17.0,~~ = 18.1,~~ P~~<<~~ 0.05, and their interaction was not significant (F = 0.4,~~0.5,~~ P > 0.05).

Mortality estimations

Mean abundances of live and dead individuals of *A. salinus~~Arctodiaptomus~~* of each developmental stage in the layers 0-15 m ($\bar{N}_i$, ~~$\bar{y}_i N_i$, y_i~~ and $\bar{y}_{i+1}$ ~~y_{i+1}~~ in Eqs 16, 17)~~6, 8)~~ and 12-15 m (y_i*~~(y*~~ in Eq. 17)~~8)~~ for calculation of NPM are presented in Table 4.~~Fig. 5.~~ Each $\bar{y}_i y_i$ value was higher than the corresponding y_i*~~y*~~ value with the two exceptions for C5. Consequently, ($\bar{y}_i - y_i$*) values were rather high and (y_i*/$\bar{y}_i$) quite low, with two exceptions (Table 4).The coefficient G, which represents carcass removal via sinking, ranged from 0.067 to 0.869 d^{-1}, with an average of 0.402 d^{-1} (SD = 0.250 d^{-1}). The coefficient D, which represents carcass removal by other processes above trap depth, ranged from 0.021 to 0.823 d^{-1}, with an average of 0.361 d^{-1} (SD = 0.244 d^{-1}) (Table 5). The~~(Fig.5). Therefore,~~ mortality rates (~~values obtained from Eq. 6 were higher than those from Eq.8 (Table 4). The values of m~~) calculated with y_i* ~~from Eq.8~~ were very low, ~~reaching negative values~~ varying from -0.009 to 0.034 d^{-1} (Table 5). Conversely, m calculated with $\bar{y}_i$ were higher, at 0.0003-0.103~~4).~~

~~NPM values from Eq. 6 (with y_i) varied within limits of 0.001-0.103~~ d^{-1} with one negative value, -0.002 (Table 5). Evidently, the negative values were within range of precision of the method, and therefore should be interpreted as ca. zero mortality. The ~~-0.001 (Table 4). The highest~~ mortality of all stages was highest at the beginning of the study, between ~~in two-day interval,~~ 19 and ~~-~~21 June (Table 5).~~4).~~ This period coincided with ~~period of~~ the occurrence of maximal percentages of dead individuals of all stages (5.3-10.3 % in 0-15 m, 25.7-83.1 % in 12-15 m), and was followed by a noticeable decrease in abundances of live animals, most noticeably~~pronounced~~ in

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nauplii, females and males ($\bar{N}_i$ ~~N_i~~ on 21 and 24 June; Table 4) ~~June, Fig.5).~~ Minimal mortality of all stages was in the last five-day period, 24-29 June (Table 5) ~~4).~~ Among all stages, females had the highest mortality (0.103-0.023 ~~(0.103–0.029~~ d^{-1}) and copepodites C5 –the lowest (0.008-0.0003 ~~ones (0.008–0.001~~ d^{-1}) (Table 5) ~~4).~~

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Discussion

~~We compared two equations to determine *in situ* non-predatory mortality *m* and to determine which of them could provide a more reliable estimate. NPM values from Eq. 6 were higher than those from Eq. 8: 0.001 – 0.103 versus 0.009 – 0.034 d^{-1}, respectively. The equations differed by a single parameter, y_i, carcass abundance above the trap (in Eq.6) or y^*, carcass abundance at the trap depth (in Eq.8). The ratio y_i/y^* for nauplii, C1-4, males and females of *Arctodiaptomus salinus* varied from 2 to 27 and for C5 from 0.6 to 13.5. Both y_i and y^* were estimated with accuracy and precision of the same order of magnitude as those of field sampling counting, for instance, with a relative error (RE) of 12.5–100% (Dubovskaya et al., 2003). Error (*Er*) of abundance estimation (*A*) by our net method with 3m hauling can be calculated as $Er = 2.01A^{0.78}$ (Gladyshev, 1985; Dubovskaya, 1987). This *Er* includes micro-horizontal variability (zooplankton patchiness).~~

Consideration of trap performance

~~For data of N_i, y_i, and y^* (Fig. 5), *Er* calculation yielded RE within a range of 20–109%. RE of y^*_{av} in Table 1 (for sinking velocity calculation) varied within limits of 0–81.2 %. The same RE of y^*_{av} for *Bosmina* in Lake Stechlin ranged from 1.3 to 66.2% (Dubovskaya et al., 2015). Although precision (variability) of *Arctodiaptomus* y^* and Y is higher in a few cases than that of *Bosmina* y^* and Y (Dubovskaya et al., 2015), sampling replications and large volumes of zooplankton samples (minimum 94 L) resulted in a reasonable accuracy of estimation of parameters in Eqs 6–8, including y_i and y^*. Thus, low y^* values did not result from lack of accuracy of their estimation.~~

~~Why is y_i greater than y^*? Non-predatory mortality in a pelagic population leaves behind carcasses in a place where the population resides. In a hypothetical quasi-stationary situation, when NPM changes with time and is equilibrate by sinking of carcasses only, the concentration of carcasses would increase with depth within the layer where zooplankton resides, or equilibrate at nearly constant value across the entire water column beneath. In reality, carcasses may remain in the water column and undergo decomposition and consumption or may rapidly sink and contribute to food source for the benthos (Tang et al., 2014). The population of *Arctodiaptomus* in Shira Lake was located primarily in the upper 0–9 m column; and the largest number of carcasses was also produced there (Fig. 3). The observed decrease in carcass abundance with depth (Fig. 3) suggests that carcass dynamics was affected by other physical processes (turbulence, density discontinuity layers) and/or biological processes like consumption and microbial degradation. As a result,~~

~~significant part of carcass abundance (y, y*) is eliminated in the water column above the traps. Below we discuss the relevance of some of these processes to the carcass abundance.~~

~~Possible bias in trap collection~~

Appropriate choice of sediment trap design and ~~,~~ dimensions is crucial~~and suspension is important~~ for avoiding under-or over-trapping (Buesseler et al., 2007). According to Lau ~~((Lau,~~ 1979), for a~~in the~~ cylindrical trap with an aspect ratio of ~~H/D~~ 6.8, resuspension starts~~started~~ when the trap Reynolds number exceeds~~exceeded~~ 15000. Given our trap dimensions and *in situ* ~~diameter of 10.3 cm,~~ kinematic viscosity of 0.017 $cm^2\ s^{-1}$, ~~at water temperature 2°C,~~ such Reynolds number is obtained only at a flow velocity of 24.7 $cm\ s^{-1}$, which is much higher than the observed flow velocity ~~observed~~ at the trap depth (3-4.6 $cm\ s^{-1}$). Thus, resuspension from our traps was unlikely. Our video ~~-~~recording also showed no~~data confirmed lack of~~ physical disturbance near the trap bottom. Another possible source of error is trap tilt resulting in over-trapping (Gardner, 1985). Our trap design according to Håkanson ~~((Håkanson,~~ 1984) kept the cylinders vertically stable irrespective of cable inclination~~; from the vertical. To avoid~~ cable motions and vibrations were further minimized by a~~,~~ subsurface tension buoy ~~was set below the depth of wave-induced motion, as Bloesch and Burns~~ (Bloesch and Burns, 1980)~~, recommended.~~ Hence, error due to trap tilt would be negligible (Gardner, 1985). Overall, the ~~our traps performed well. Trap~~ relative errors of our trap data (22-43%, Table 1) indicate good~~d common~~ trap precision (Stanley et al., 2004; Buesseler et al., 2007).

According to our data, there were no marked daily changes in the vertical distribution of dead~~carcasses~~ and live *A. salinus*~~Arctodiaptomus~~ (Fig. 3). Similarly, Zadereev and Tolomeyev (~~Tolomeev (Zadereev and Tolomeev,~~ 2007) did not observe ~~in fishless Shira Lake~~ any large-scale diel vertical migrations (DVM) of *A. salinus* in the fishless Lake Shira. Therefore,~~any stage of Arctodiaptomus. Thus, DVM could not affect~~ our sampling and calculations were not affected by DVM ~~in Eqs 6-8.~~

*Comparison of $\bar{y}$ and y**

The population of *A. salinus* was concentrated in the upper 0-9 m, where the largest number of carcasses was also found (Fig. 3). The observed decrease in carcass abundance with depth (Fig. 3) is consistent with the study of Bickel et al. (2009), and suggests that carcass dynamics was affected by processes other than sinking. Both $\bar{y}$ and y^* were estimated with accuracy and precision of the same order of magnitude as those of other field studies (e.g. Dubovskaya et al., 2003). Error (Er) of abundance estimation (A) by our net sampling method can be calculated as $Er = 2.01A^{0.78}$ (Gladyshev, 1985; Dubovskaya, 1987). This Er includes micro-horizontal variability (zooplankton

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patchiness). For data of $\bar{N}_i$, $\bar{y}$ and y^* (Table 4), *Er* was within a range of 20-109%. *Er* of y^*_{av} in Table 1 (for sinking velocity calculation) varied within 0-81.2 %, comparable to that for *Bosmina* in Lake Stechlin (1.3-66.2%; Dubovskaya et al., 2015). Although y^* and Y were more variable in a few cases than those reported by Dubovskaya et al. (2015), sampling replications and rather large volumes of zooplankton samples (≥ 94 L) gave a reasonably accurate estimation of $\bar{y}$ and y^*.

Except for two occasions, y^* was in all cases lower than $\bar{y}$, giving low averaged $y^*/\bar{y}$ values of 0.13-0.19 for all stages except C5 (0.77; Table 4). This observation has important ramifications for understanding NPM and carcass dynamics in the lake. Given $\bar{y}>y^*$, it means that many carcasses were removed from the water column before they reached the traps. Under such a condition, the choice of proper formulations is crucial for NPM calculation. When applying Eq. 17 to our data, NPM was-0.009-0.034 d^{-1}; while using Eq. 16 increased NPM estimation to -0.002-0.103 d^{-1} (as explained above, the negative values should be interpreted as zero mortality within the range of precision of the method).The latter values are more realistic, since they follow from the assumption of non-negligible D, which is also supported by $\bar{y}>y^*$ in our observations (see Introduction and Methods). Hence, application of Eq. 17 to sediment trap data would underestimate NPM. Even a small difference in NPM, when propagating through time, could lead to vastly different population growth projections (Elliott and Tang, 2011).

Carcasses in the water column can be removed e.g. by detritivory or microbial degradation. Turbulent mixing can increase the retention time of carcasses in the epilimnion and decrease the ratio $y^*/\bar{y}$. The coefficients G and D were strongly correlated and comparable to each other (linear regression: $D = 0.974\ G - 0.030$; $r^2 = 0.992$), suggesting that both sinking and water column processes were equally important in eliminating carcasses. The coefficient D in our calculations encapsulates the combined effect of different water column processes, but it does not distinguish their relative importance. Nevertheless, below we use independently collected data to examine the roles of these processes in removing zooplankton carcasses above the trap depth.

Possible ingestion of carcasses by Gammarus ~~**predation effects**~~

The amphipod ~~zone of~~ *Gammarus lacustris* was the main predator in the fishless Lake Shira. Consistent with the~~habitation is the 0-12 m column (Table 2), which corroborates~~ data by Zadereev et al. (Zadereev et al.,-2010) and Tolomeyev~~Tolomeev~~ et al. (Tolomeyev~~(Tolomeev~~ et al., 2006), *G. lacustris* occupied the 0-12 m layer, but not below (Table 2).~~2006).~~ Therefore, *G. lacustris* would~~*Gammarus* could~~ not affect *A. salinus*~~*Arctodiaptomus*~~, carcass abundance at~~in~~ the trap depth. Rare~~12-15 m layer (y^*). As our traps were suspended below the zone of *Gammarus* occupation, rare~~ appearance of *G. lacustris*~~one individual per trap could not substantially affect the carcass abundance in the traps (Y). Video registration~~ inside the traps also suggests that this predator had

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showed no effect on carcass abundance in the traps or *Gammarus* presence there. Thus, *Gammarus* did not affect our calculation of carcass *Arctodiaptomus* sinking velocity from trap data and *G.*

Previous studies in Lake Some researchers of Shira have shown *G. lacustris* Lake ecosystem consider pelagic *Gammarus* as the top predator of feeding on live and dead individuals of *A. salinus* *Arctodiaptomus* and Rotifera in from the epi-and meta-limnion epi-metalimnion (Yemelyanova et al., 2002; Gubanov, 2009). We found *A. salinus* *Arctodiaptomus* remains in the guts of *G. lacustris* from the net and trap samples. Although we could not determine the original vital state of the ingested *Gammarus* individuals, our observations at least indicate that the amphipod from the lake and trap samples, thus confirming predation of the former by the latter. *G. lacustris* can capture and consume diaptomid copepods (Wilhelm and Schindler, 1999; Yemelyanova et al., 2002). Thus, *Gammarus* could potentially ingest *A. salinus* consume live and dead *Arctodiaptomus* in the 0-12 m column, decreasing the number of *Arctodiaptomus* carcasses above the trap depth and contribute to the removal coefficient *D*.

The that had reached the 12-15 m layer, i.e. lowering not only y_i, but also y^*. This potential loss of carcasses due to ingestion by *G. lacustris* could be estimated from the as daily minimal consumption compensating daily energy expenditure of the amphipod. An individual of *G. lacustris* with a body length of *Gammarus* 10 mm long weighs ca. 11.60 mg (Yemelyanova et al., 2002) and has a respiration rate of 4.2 µl O_2 ind^{-1} h^{-1} at the epilimnic mean temperature of 20 20°C (Sushchenja, 1972). Its Assuming maximal abundance of the both species in the 0-6 m epilimnion at the epilimnetic mean temperature of 20 °C, we estimated the daily energy expenditure can be estimated as $R = (0.0042 \times 24 \times 4.86)/0.9 = 0.544$ mg $ind^{-1}day^{-1}$, where 4.86 cal ml^{-1} O_2 is oxycaloric coefficient and 0.9 cal mg^{-1} is caloric content of wet mass (Winberg, 1986). Assuming an assimilation efficiency of 0.8 (Winberg, 1986), the required prey consumption would be 0.680 mg $ind^{-1}d^{-1}$ $ind^{-1}day^{-1}$. Given a wet weight of 0.068 mg for adult *Arctodiaptomus* 1.2 mm long (Balushkina and Winberg, 1979), this is equivalent translates to a consumption of ~10 carcasses ind^{-1} d^{-1}. The maximal day^{-1}. Maximal abundance of *G. lacustris* *Gammarus* in the 0-12 m layer was column, 29 ind m^{-3}, which translates to a maximal removal of 290 ind m^{-3} could consume 290 carcasses of adult *A. salinus* carcasses. *Arctodiaptomus*. This estimated value is comparable to with the averaged difference between $\bar{y}_i$ and y^*, whose values for females and male *A. salines* carcasses (242 and 249 s fall within the limits of 54-684 ind m^{-3}, with the mean of 222 ± 40 ind m^{-3}, respectively; Table 4). Therefore, ingestion of carcasses by *G. lacustris* within 0-12 m could explain the loss of carcasses. m^{-3}. Thus, *Gammarus* predation could be a potential cause why part of carcass number of y_i did not reach the 12-15 m layer and y^* was < y_i.

Turbulence effect and microbial decomposition

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Among the~~Sinking velocity~~

~~The *in situ* sinking velocities of *Arctodiaptomus* carcasses obtained from our trap data (Table 3) are comparable with those of *Cyclops vicinus* carcasses in a small Siberian reservoir (0.3-5.8 m d^{-1}) measured by the same method (Dubovskaya et al., 2017). In the rank of~~ nauplii, C1-4 and adults, the average carcass sinking velocity (v*)~~averages~~ increased ~~from 3.7 to 9.3 m d^{-1};~~ in accordance with the increase in body~~the stage~~ size. An interesting exception was C5, which had the lowest carcass~~However, the~~ sinking velocity and it is likely due to the presence of fat droplets in its body~~of the large-sized C5 is left out of this rank, having the minimal average of 2.0 m d^{-1}. Apparently, this low v* is the result of the lower C5 body density due to presence of light fat inclusions~~ (e.g. Stepanov and Svetlichnyyi,~~Svetlichny,~~ 1981). The presence of ~~For instance, an increase in the~~ fat droplet may allow C5 (both live and dead) to ~~volume in bodies of *Calanus helgolandicus* resulted in a decrease in their density from 1.07 to 1.02-1.015 g cm^{-3} (Stepanov and Svetlichny, 1981). Water densities of Shira Lake in the 6-12 m layer were similar, 0.015-0.012 g cm^{-3} (Fig. 2C). So in this layer, C5 might~~ achieve neutral buoyancy ~~(excess density = 0), which might result in accumulation of live~~ and congregate within ~~dead C5 individuals in the~~ 6-12 m as observed in our field sampling.

The *in situ* carcass sinking velocities of *A. salinus* (2.0-8.5 m d^{-1}) were in general much lower than those obtained by *in vitro* settling column method. For example, *in vitro* sinking velocity was 35.4±15.6 m d^{-1} for *Acartia tonsa* C1-3~~layer. Besides, C5~~ carcasses (Elliott et al., 2010), and 112.1±20.3 m d^{-1} for *Eudiaptomus gracilis* adult carcasses (Kirillin et al., 2012). *In vitro* sinking velocity in the absence of any water motion and physical gradients should be regarded as «maximal» (Ploug et al., 2008), or «potential» sinking velocity (Grossart and Simon, 1998). In contrast, *in situ* sinking velocity calculated from Eq.4 represents the average downward velocity of sinking and suspended particles (McDonnell et al., 2010; 2015). Carcasses may~~might~~ achieve positive buoyancy due to microbial decomposition and float upward (Elliott et al., 2010; Kirillin et al., 2012)—a phenomenon known as~~2012). Causes of the~~ "anti-rain" of carcasses ~~were discussed elsewhere~~ (Dubovskaya et al., 2015), and not be captured by the traps.~~2015).~~

Wind-driven currents and turbulence may also decrease ~~The *in situ*~~ carcass sinking velocities, leading to ~~of *Arctodiaptomus* (2.0-9.3 m d^{-1}) were much lower than those obtained by *in vitro* settling column method. For example, *in vitro* sinking velocity of *Acartia tonsa* copepodites I-III was 35.4±15.6 m d^{-1} (Elliott et al., 2010), and that of *Eudiaptomus gracilis* adults 112.1±20.3m d^{-1} (Kirillin et al., 2012). *In vitro* sinking velocity in the absence of any water motion and physical gradients is named as «maximal» (Ploug et al., 2008), or «potential» sinking velocity (Grossart and Simon, 1998). As for *in situ* sinking velocity in Eq 4, it is "the average downward velocity of all the particles present in a given size class", which includes both sinking and suspended particles (McDonell et al., 2010 p. 2086). Hence, this velocity (w) "is~~ a lower average v* and a lower

mortality rate that can be accounted for by carcass sinking. During our study, wind speed increased~~limit estimate of the velocity of the actively sinking particles as the presence of suspended particles would decrease *w*" (McDonell et al., 2015 p.185). We suggest that buoyancy of *Arctodiaptomus* carcasses varies with varying of the stage and time after death. Then neutrally and positively buoyant carcasses outside the trap are included in *y** but not collected by the trap and not included in *Y*, thus lowering average *v** from Eq 4.~~

~~Our data also suggests an appreciable effect of the wind-driven currents and turbulence on the sinking rates: wind speed increase~~ on 21-22 June and on 25-26 June, resulting ~~was reflected~~ in ~~the~~ high-amplitude oscillations of the isotherms—indicator of intensified internal wave activity, and a~~in the~~ ~3-fold increase in~~of the~~ current speeds at the trap depth (Fig.2A). Sinking ~~depth of traps exposure. Although the resolution of observations does not allow deriving a statistically significant effect, sinking~~ of carcasses might be slowed down by ~~the~~ shear turbulence during these periods. Indeed, on 24-26 June the traps yielded rather low values of carcass sinking velocity, especially trap No. 1 and 2 (Table 3). Minimal sinking velocity of male carcasses was obtained in this period (Table 3). This turbulence effect has been described by others:~~is also known from previous studies:~~ Dubovskaya et al. (Dubovskaya et al., 2003) showed that the~~negative relationship of~~ sinking velocities of *Daphnia* and *Cyclops* carcasses (v, m d^{-1}) were negatively correlated with wind speed (u, m s^{-1}) as~~over the reservoir:~~ $v = 3.709u^{-0.984}$. Ivory et al. (Ivory et al., 2014) also found a~~obtained~~ negative relationship between carcass flux measured by traps (y, mg C $m^{-2}day^{-1}$) and mean current velocity at the trap depth (x, cm s^{-1}): $y = 105.9e^{-0.70x}$. ~~Modeling of sinking velocity of zooplankters with turbulence and temperature parameters in a lake also showed that in lake conditions, the laboratory settling column velocity decreased by a factor of two (Kirillin et al., 2012; Dubovskaya et al., 2015).~~

We~~Based on this, we may~~ suggest that turbulence increases the retention time of carcasses in the upper epilimnion, where they can be removed~~are further eliminated~~ by ingestion~~decomposition~~ and/or microbial degradation. Based on the measured~~ predation. At~~ mean sinking velocities ~~(given in~~ Table 3),~~3,~~ carcasses of nauplii from the surface (z = 0 m) would reach the sediment trap at ~~and C1-4 would sink to the~~ 14 m in ~~depth for~~ 3.8 ~~and 2.7~~ days, C1-4~~respectively, and male or female~~ carcasses in 2.7 days, and adult carcasses in~~for~~ 1.5 days. During this time, microbial degradation as a temperature-dependent process (Eq. 18 in Kirillin et al., 2012) would~~The~~ decrease the ~~in~~ carcass excess density by respectively ~~during this time at 20°C will be~~ 0.0223, 0.0210 and 0.0188 g cm^{-3}. Assuming an ~~based on Eq. 18 in (Kirillin et al., 2012). Estimating the~~ initial carcass density of~~as~~ 1.045 g cm^{-3} (Elliott et al., 2010), microbial degradation would lower the carcass excess density by 50,~~the decrease will be 50%,~~ 47 and 42%~~, of excess density,~~ respectively. Such a substantial loss~~significant lowering~~ of excess density would greatly~~down to zero at minimal sinking velocities~~

~~will~~ increase carcass retention time and remineralization above~~of carcasses in~~ the traps.~~0-12 m column until their full mineralization (at least to an empty chitin carapace).~~

The estimates of ~~the~~ turbulent mixing from the flux-gradient method (Fig.2D) also suggest high mixing rates in the epilimnion, apparently driven by wind. The~~wind: the~~ K_Z values in the upper mixed layer of Lake Shira are up to one order of magnitude higher (10^{-1} m^2 s^{-3}) than those measured previously in the similarly sized but more wind-sheltered Lake Stechlin ~~having similar spatial dimensions~~ (10^{-3}-$10^{-2}$$m^2$ s^{-3}, Kirillin et al., 2012). Interestingly, ~~Noteworthy,~~ according to the random-walk model of turbulence (Kirillin et al., 2012), this increase of K_Z does not produce any significant increase in carcass retention in the epilimnion. Apparently, isotropic chaotic movements have little effect on carcass sinking. However,~~of the carcasses retention in the epilimnion. Shortcomings of the random-walk method in application of turbulence are the main reason for this result: the effect of wind on the vertical particle motion is more manifold than simple intensification of stochastic vertical motions. In particular,~~ the circular water motions produced by surface waves, Langmuir circulations, or convective cells may capture relatively small ~~the~~ particles (e.g. zooplankton carcasses)~~of comparably small size~~ for a longer time and ~~may also~~ contribute to their mechanical destruction. A reliable quantification of these effects requires *in situ* observation of carcasses movement in surface waters.~~registration of carcasses movement in surface waters. The stratification in Shira is also appreciably stronger than in freshwater lakes, where similar works were previously performed (Kirillin et al., 2012; Dubovskaya et al., 2015): the density jump across the Shira pycnocline is ~5 kg m^{-3} vs. ~2 kg m^{-3} in Lake Stechlin and Arendsee, which factor can further slowdown carcasses sinking and promote their degradation in the water column. Extrapolation of the particle sinking model used by Kirillin et al. (Kirillin et al., 2012) and Dubovskaya et al. (Dubovskaya et al., 2015) on *Arctodiaptomus* sinking in Lake Shira produces however the sinking velocities of 10-100 m d^{-1}, which are much higher than those following from the sedimentation trap data. The reasons for this divergence between the field observations and the modeling results based on *in vitro* data were discussed previously (Dubovskaya et al., 2015). In brief, the purely known degradation rates, the lack of adequate description for the vertical water motions, and missing the uncertainties in estimation of the excess density of carcasses relative to that of water are among the major reasons of overestimated model sinking velocities.~~

The stratification in the brackish Lake Shira is appreciably stronger than in freshwater lakes. For example, the density difference across the Lake Shira pycnoclinewas~5 kg m^{-3}, compared to only ~2 kg m^{-3} in Lake Stechlin and Lake Arend (Kirillin et al., 2012). The strong stratification in Lake Shira could further slowdown carcass sinking and promote their degradation in the water column.

Reality check of non-predatory~~non-predation~~ mortality estimates

The decrease in carcass~~of the carcasses~~ abundance with depth indicates that a significant amount of carcasses was eliminated ~~is eliminated in the water column above the traps. Formally, this fact implies that Eq. 1 and its derivatives, Eqs 6 and 8, are inapplicable in this situation without introducing a new 'sink term' describing the cumulative effect of mechanical destruction, biodegradation and consumption. In the current form, Eq. 1 incorporates all these elimination effects in the 'source term' mN, thus reducing the mortality estimation m compared with the actual *in situ* mortality, potentially to zero or even to negative values, if the carcasses production on the traps' depth is higher than the flux~~ from the water column above the traps. ~~above. Indeed, from Eq. 8, we obtained extremely low NPM (−0.009 – 0.034 d^{-1}) including 5 negative values (Table 4).~~ However, the processes of carcass~~es~~ elimination are ~~extremely~~ difficult to parameterize due to limited observational information, and the removal term remains poorly constrained.~~such a 'sink term' would be quite uncertain.~~ Only a rudimentary approach~~es~~ to this problem was attempted by ~~are realizable at the current state of knowledge, like that of~~ Frangoulis et al. (Frangoulis et al., 2011), who attributed the ~~introduced such a term in a simplest form, as a~~ decrease in ~~of~~ carcass flux with increasing~~an increase in the trap~~ depth ~~due~~ to decomposition of the sinking material. Hence, the reliability of the otherwise well-established and robust sedimentation trap method to estimate ~~estimation of the~~ zooplankton NPM ~~mortality~~ requires a more thorough evaluation. ~~examination. We have shown that low carcass abundance at the trap depth, y*, could be the result of sinking of carcasses from the 0–12 m column which have escaped predation and decomposition and reached the lower layer (12–15 m). In addition, a few carcasses could be produced in the 12–15 m layer by a few live animals staying here. The resulting y* value will be lower than the y, value, which reflects the number of carcasses produced in the column of primary residence of the population.~~

Incorporation of removal processes in addition to sinking (Eqs. 9 and 16) to derive conservative estimates of NPM produces NPM values of 0.0003. ~~The question, which of the two equations, 6 and 8, is more reliable in application to the estimation of non-predation mortality can be answered by a closer inspection of Equation 5, which can be rewritten in the originally measured variables as,~~

~~$$m = \frac{1}{\bar{N}}\left(\frac{\partial \bar{y}}{\partial t} + \frac{Y}{hS}\right) \qquad (12)$$~~

~~corresponding exactly to Eq. 8, the latter therefore being the only correct form of Eq. 1 in application to the sediment traps measurements. On the other hand, the NPM values derived from Eq. 6 (0.001 –~~ 0.103 d^{-1}, which ~~d^{-1}) seem to be more realistic, and~~ are comparable to the non-predatory mortality~~physiological death~~ rates for zooplankton reported in~~known from~~ the literature (<0.01-0.15 d^{-1}; reviewed by Tang and Elliott, 2013). For example, the rich fat content observed in ~~In particular, minimal m of diapausing~~ C5 was indicative of diapause, and the estimated m for C5

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(0.0003-0.008(0.001 d^{-1}) was indeed closeequal to the minimal physiological death rate of 0.001-0.05 day^{-1} (Shushkina et al., 2000; Dubovskaya, 2009).Two of the three *m* values for 2009), and minimal *m* of females (0.048-0.023) and (0.066-0.029) or all *m* of males (0.049-0.020), on the other hand, (0.049-0.029) were close to the upper limit of senescencethe senescent death rate of 0.01-0.05 day^{-1} (Tang et al., 2014). The same range of NPM values was reported by Frangoulis et al.is given (Frangoulis et al., 2011) for copepodsnon-predatory mortality of copepod biomass derived from "swimmer--excluding" sediment trap data. The minimal mortality of adults of calanoid copepods in survival experiments was also within the range of 0.001-0.031 d^{-1} (Kiørboe et al., 2015). -2015). Tang and Elliott (Tang and Elliott, 2013) in their review reported limits of 0.01—0.065 d^{-1} for known values of NPM. The highest NPM values 0.103 and 0.100 d^{-1}were obtained for copepodites 1-4 and females during the first interval of mortality calculation (19-21 June). The most likely causes of younger stage deaths might be high temperature (Jiménez-Melero et al., 2007; Elliott and Tang 2011), lack of food quality and quantity and /or diseases and parasites (Dubovskaya, 2009; Tang et al., 2014). Given the occurrence in our samples of *Arctodiaptomus* adults similar to ones with the "white fat cell disease" (Ebert, 2005), micro-parasite infection was the most likely cause of high NPM of females in addition to physiological senescence.

Furthermore, the temporal variationdynamics of NPM values from Eq. 6 was consistent with *A. salinus*concurrent *Arctodiaptomus* abundance data. For example, the relativelyIndeed, comparatively high mortality of all developmental stages (the population average 0.061 d^{-1};d^{-1}, Table 5)4) at the beginning of the study period (19-21 June) was followed by aled to some decrease in the abundance of live nauplii, C1-4, males and females between 21 and 24 June(Table4). (Fig.5). During the following 5-day intervals Δt_2 and Δt_3, the, NPM value decreased initially to 0.022s were low (0.029 and 0.009 d^{-1}on average) and to 0.007 d^{-1}afterwards, andfell within the concurrent physiological death range. Concurrent variations in the abundance of all developmental stages were also rather low, suggesting that the population was close to equilibrium.

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Conclusion

Notwithstanding the ignorance of zooplankton carcasses in conventional field sampling, it is now evident that zooplankton can suffer, at times significantly, non-predatory mortality and leave behind carcasses. Sediment trap method has been well developed and widely used for studying sinking fluxes. By using sediment traps to collect sinking zooplankton carcasses *in situ*, it is possible to derive NPM from the trap data, as well as to assess the contribution of zooplankton carcasses to organic carbon flux. Hence, sediment traps, when augmented by water column sampling, provide an effective means to investigate zooplankton non-predatory mortality and the fate of the carcasses.However, the sediment trap method assumes sinking as the major (sole)

process removing carcasses. Accordingly, the accuracy of the method can be compromised when carcasses are removed by other processes in the water column before they reach the traps.

In this study, we began with a detailed mathematical analysis of the problem and derived formulations to account for carcass removal from the water column. We then used an empirical study in Lake Shira to compare and contrast the use of depth-integrated average carcass abundance ($\bar{y}$) and depth-specific carcass abundance (y^*) for calculating NPM of the dominant copepod *A. salinus*, and to examine the different water column processes for removing copepod carcasses. We showed that in Lake Shira where carcass abundance decreased with depth, it is essential to take into account removal of carcasses in addition to sinking when calculating NPM. To a first approximation, it can be done by adopting the mean abundance of carcasses in the water column above traps as a characteristic value for estimation of the NPM from the trap data. We also showed that ingestion by the amphipod *G. lacustris*, along with turbulent mixing and microbial degradation, could account for the estimated removal of carcasses above trap depth.

The observation that y^* was considerably smaller than $\bar{y}_I$ means that a good portion of the zooplankton carcasses was retained in the upper water layer, thereby contributing to epilimnic carbon and nutrient cycling, rather than to the benthic food web in Lake Shira.

~~In order to qualify the validity of Eq. 6 in application to the NPM estimation, let us consider a simplified case of depth-constant sinking velocity v. Then, Eq. 1 turns into~~

~~$$\frac{\partial y}{\partial t} = mN - v\frac{\partial y}{\partial z} \quad (13).$$~~

~~Assuming further the live zooplankton is equally distributed across the water column (N=const), and the situation is close to steady state ($\partial y/\partial t \approx 0$), Eq. 1 solves as~~

~~$$y = (mN/v^*)z + y_0 \quad (14)$$~~

~~i.e. abundance of carcasses y should linearly grow with depth. Note that at these conditions, Eq. 1 produces zero mortality rate m if distribution of carcasses is vertically homogeneous, $\bar{y} = y^*$. That means, a steady-state situation with an equally distributed abundance of carcasses is impossible, unless degradation of carcasses takes place, which then should be incorporated into Eq. 1. The degradation rate D can be incorporated into the vertical transport of carcasses (Eq. 1) as follows~~

~~$$\frac{\partial y}{\partial t} = mN - v\frac{\partial y}{\partial z} - Dy \quad (15).$$~~

~~Solution of Eq. 15 yields exponentially decaying abundance of carcasses with depth. To find its connection to the estimations of the mortality rate m, based on Eq. 6, let us assume the instant abundance of carcasses is proportional to the abundance of live zooplankton, $y = \delta N$. The analytical solution of Eq. 15 under the same assumptions N = const and $\partial y/\partial t \approx 0$ reads~~

$$y(z) = y_0 \exp\left(\frac{m - D\delta}{\delta v} z\right) \quad (16)$$

and the discrete numerical solution with regard to m, analogous to Eq. 8 can be written as

$$m_i - D\frac{y_i}{N_i} = \frac{\Delta y}{\Delta t N_i} + G_i \frac{y^*}{N_i} \quad (17).$$

Thus, in presence of carcasses degradation, the mortality rate m_{trap} calculated by Eq. 6, 8 from sediment trap data is, in fact, reduced by relative degradation rate, as compared with the real mortality *in situ*:

$$m_{trap} = m - D\frac{y}{N}.$$

Apparently, the slower the degradation D the closer is the trap estimation to the real mortality. Using the nearly exponential vertical distribution of carcasses, as follows from Eq. 16, one can estimate the error introduced by using Eq. 6 instead of Eq. 8, i.e. by replacement of the carcasses abundance at the trap depth y^* with the mean abundance above the trap $\overline{y}$. Introducing $\gamma = (D - m/\delta)/v$, one can show that $\overline{y} / y^* \to 1$ at $\gamma h \to 0$, and $\overline{y} / y^* \to \infty$ at $\gamma h \to \infty$, where h, as before, is the depth of the trap exposition. Hence, Eqs 6 and 8 are interchangeable if the traps are positioned close to the depth of the maximum abundance of zooplankton as in (Dubovskaya et al., 2015), and the error becomes higher with deeper exposition of traps. An intermediate case $\gamma h \simeq 1$ yields $\overline{y} / y^* \simeq (e - 1) \simeq 1.71$, i.e. Eq. 6 would in typical configurations slightly overestimate the mortality rate, which overestimation is however within the range of the method accuracy.

Conclusions

We can conclude that Eq. 6 is applicable to the mortality rate estimations and may be preferred in the analysis of field data, as having one important advantage: at low abundances of carcasses on the depth of trap exposition (y^*), the integral sample $\overline{y}$ (y_t) would provide more reliable numbers than small samples from a single depth. Values of NPM of *Arctodiaptomus*, determined by the equation with y_t, were 0.001–0.103 d^{-1}, and were in good agreement with literature data and the population abundance dynamics. NPM values from the equation with y^* (Eq. 8) were too low to be realistic. A considerable decrease in y^* compared with y_t ($y_t > y^*$) means that zooplankton carcasses in deep stratified lakes are mostly eliminated via consumption and microbial decomposition in upper layers of the pelagic zone, rather than by sinking through the thermocline to the bottom. Thus, they contribute to pelagic carbon mineralization and nutrient recycling, rather than to benthic food webs.

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Table 1. Number of *Arctodiaptomus salinus* carcasses accumulated in sediment traps per day (Y, ind d^{-1}) and carcass abundances at trap depth, 12-15 m, average of 2-3 samples taken at the beginning and the end of daily trap exposure (y^*_{av}, ind m^{-3}) in Lake Shira ~~Lake~~ (for calculation of v^*).

Date in June	Carcasses in sediment trap, Y					Carcasses at trap depth (12-15 m), y^*_{av}		
	Trap1	Trap2	Trap3	*CV* (%)	*RE* (%)	Abundance	*CV*(%)	*RE* (%)
Nauplii								
18-19	nd	5	15	70.7	50	127	nd	nd
19-20	20	14	20	19.25	11.1	167	33.9	24
20-21	41	20	23	40.6	23.4	210	1.7	1.2
24-26	~~0.5~~1	~~0.5~~1	~~1~~2	43.3	25	49	12.9	7.4
26-27	6	1	nd	101	71.4	69	32.8	23.2
27-28	1	0	nd	141.4	100	154	63.4	44.8
28-29	1	0	1	86.6	50	85	140.7	81.2
Mean	-	-	-	-	47.2	116.9	-	36.2
C1-4								
18-19	nd	5	9	40.4	28.6	64	nd	nd
19-20	9	9	11	12	6.9	83	31.7	22.4
20-21	33	12	33	46.6	26.9	146	43.6	30.8
24-26	~~36~~	~~36~~	~~2.5~~	10.2	5.9	81	15.6	9
26-27	13	12	nd	5.7	4	154	73.5	51.9
27-28	10	4	nd	60.6	42.9	483	72.9	51.6
28-29	7	2	4	58.1	33.5	329	106.9	61.7
Mean	-	-	-	-	22.1	200.8	-	37.6
C5								
18-19	nd	1	2	47.1	33.3	21	nd	nd
19-20	7	2	4	58.1	33.5	88	107.5	76
20-21	17	4	1	116	67	152	2.3	1.7
24-26	~~1~~2	~~0~~	~~1.5~~3	91.7	52.9	134	50.7	29.3
26-27	1	4	nd	84.9	60	165	40.8	28.9
27-28	2	7	nd	78.6	55.6	128	11.6	8.2
28-29	1	1	1	0	0	81	72	41.6
Mean	-	-	-	-	42.5	107.5	-	27.4
Females								
18-19	nd	2	8	84.6	60	21	nd	nd
19-20	13	8	9	26.5	15.3	48	78.9	55.8
20-21	24	8	6	77.9	45	74	0	0
24-26	~~24~~	~~12~~	~~36~~	50	28.9	25	48.5	28
26-27	3	4	nd	20.2	14.3	37	19.1	13.5
27-28	2	5	nd	60.6	42.9	48	16.4	11.6
28-29	1	6	3	75.5	43.6	28	77.4	44.7
Mean	-	-	-	-	36.3	37.8	-	21.9
Males								
18-19	nd	5	5	0	0	21	nd	nd
19-20	14	8	7	39.2	22.6	56	88.4	62.5
20-21	20	8	11	48	27.7	72	37.3	26.4
24-26	~~24~~	~~0.5~~1	~~24~~	57.7	33.3	25	48.5	28
26-27	2	3	nd	28.3	20	27	82.7	58.5
27-28	2	5	nd	60.6	42.9	64	47.9	33.9
28-29	7	8	5	22.9	13.2	42	100	58
Mean	-	-	-	-	26.8	43.6	-	38.2

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Table 2. Number of *Gammarus lacustris* in the net column samples (ind. sample^{-1}), at trap depth and inside the traps, Lake Shira, ~~Lake,~~ 2015, dash – no samples.

Date in June	Water column					Trap depth	In traps		
	0-3 m	3-6 m	6-9 m	9-12 m	0-12 m	12-15 m	1	2	3
18	-	-	-	-	7	0	-	-	-
19	-	-	-	-	4	0	0	0	1
20	-	-	-	-	-	0	0	1	0
21	2	1	2	0	-	0	1	1	0
24	0	1	0	1	-	0	-	-	-
24 night	1	1	0	0	-	0	-	-	-
26	-	-	-	-	11	0	0	0	0
27	-	-	-	-	8	0	0	0	0
28	-	-	-	-	5	0	0	0	0
29 night	4	4	1	0	-	0	-	-	-
29	1	4	1	1	-	0	0	0	0

Table 3. *In situ* sinking velocity (v*, m d^{-1}) of *Arctodiaptomus salinus* carcasses calculated from Eq. 4 using data from Table 1 for Lake Shira. ~~Lake, means labeled with the same latter are not significantly different at P<0.05 after ANOVA post-hoc Fisher test.~~

Date in June	Trap No	Nauplii	C 1-4	C5	Females	Males
18-19	1	2.36	4.69	2.86	5.72	14.29
	2	7.09~~7.08~~	8.44	5.72	22.87	14.29
19-20	1	7.19	6.55	4.80	16.43	15.01
	2	5.03	6.55	1.37	10.11	8.57
	3	7.19	8.00	2.74	11.37	7.50
20-21	1	11.75	13.57	6.74	19.47	16.67
	2	5.73	4.93	1.58	6.49	6.70
	3	6.59	13.57	0.40	4.87	9.17
24-26	1	0.61~~1.22~~	2.21~~4.43~~	0.45~~0.89~~	4.80~~9.60~~	4.80~~9.60~~
	2	0.61~~1.22~~	2.21~~4.43~~	0	2.40~~4.80~~	1.20~~2.40~~
	3	1.22~~2.44~~	1.85~~3.69~~	0.67~~1.34~~	7.20~~14.41~~	4.80~~9.60~~
26-27	1	5.22	5.07	0.36	4.87	4.53
	2	0.87	4.68	1.46	6.49	6.80
27-28	1	0.39	1.24	0.94	2.53	1.89
	2	0	0.50	3.30	6.32	4.73
28-29	1	0.71	1.28	0.74	2.12	9.93
	2	0	0.36	0.74	12.73	11.35
	3	0.71	0.73	0.74	6.36	7.10
Mean ±		3.51±0.82~~3.65±~~	4.81±0.97~~5.15~~	1.98±0.47~~2.04~~	8.51±1.40~~9.31~~	8.30±1.07~~8.90~~

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SE	~~0.80^{AB}~~	~~±0.93^{B}~~	~~±0.46^{A}~~	~~±1.38^{C}~~	~~±1.00^{C}~~
For mortality calculation					
19-21	6.62±0.93	8.29±1.24	3.28±0.80	12.16±2.38	11.52±1.39
21-26	4.42±1.82~~4.82±~~	6.39±3.58~~7.44~~	1.64±1.04~~1.83~~	7.54±2.48~~9.94~~	7.23±2.17~~9.02~~
	~~1.67~~	~~±1.95~~	~~±1.01~~	~~±2.41~~	~~±1.90~~
24-29	1.03±0.48~~1.28±~~	2.01±0.52~~2.69~~	0.94±0.29~~1.05~~	5.58±0.99~~7.02~~	5.71±1.01~~6.79~~
	~~0.49~~	~~±0.62~~	~~±0.28~~	~~±1.29~~	~~±1.05~~

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Table 4. Weighted mean abundances (ind m^{-3}) NPM values (m, d^{-1}) of live and dead *Arctodiaptomus salinus* in 0-15 m water column and at trap depth, 12-15 m, in Shira, Lake Shira. For m calculations, data on 19, 21, 24, 26, 29 June were used (in bold). calculated from Eq.6 and Eq.8.

Date in Periods of June	0-15 m From Eq. 6 (with y_i)		12-15 m From Eq. 8 (with y^*)			$\bar{y}_i - y_i^*$	$y_i^*/\bar{y}_i$		
June Nauplii	Live ($\bar{N}_i$)	Dead ($\bar{y}_i$)	Live (N*)				Dead (y_i^*)		
Nauplii 19-21	0.044		0.006						
19-21-26			2056		1	1929			
	238850.012		0.009	244	2		0.06		
20-24-29	nd-0.001		nd-0.004		7	nd			
				42	2		nd		
21-C1-4		22			0			21	1990
	33158	02			7			2	0.10
24-19-21			5020.0	202	1672	454	0.10		
	168280.100		34		4				
21-**26**			397-		8				
					5	344			
	126420.039		0.007	180	3		0.13		
27-24-29			2660.0		8	181			
	120400.008		002	488	5		0.32		
28-C5		43						22	210
	10842	3			467			3	0.54
29-19-21	77330.008		1510.0	180	1	135	0.11		
			001		6				
Mean±SE 21-26	-0.001		-0.004	-	-	749±315	0.19±0.07		
C1-4-24-29	0.001		0.0002						
19-Females		17							1642
	14928	06			191			64	0.04
20-19-21	nd0.103		nd0.007		1	nd			
					0				
				42	1		nd		
21-26					1	2467			
			2658 0.001	159	9				
	285350.066			2	1		0.07		
24-29			1132 0.006	223	8	1047	0.08		
	255200.029				5				
26-Males		10							1024
	24625	98			382			74	0.07
27-19-21					2	1017			
			1251 0.023	129	3				
	286560.049			5	4		0.19		
28-21-26					7	1554			
			2286-	196	3				
	457750.028		0.006	4	2		0.32		
24-29	256150.010		10800.	653	1	952	0.12		
			003		2				

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Mean±SE~~Population mean~~	-	-	-	8 -	-	-	1386±209	0.13±0.04
C5~~19-21~~								
	~~0.061~~	~~- (not calculated)~~						
~~19~~21-26	7535~~0.029~~	284~~-~~	106	2 1	263	0.07		
2024-29	nd~~0.009~~	nd~~-~~		1 5	nd			
			446	4		nd		
21	3094	276			1672	149	127	0.54
24	3180	138			1290	96	42	0.70
26	5429	119			1932	212	-93	1.78
27	4899	94			1274	117	-23	1.25
28	5432	257			1285	138	119	0.54
29	2953	106			956	53	53	0.50
Mean ±SE	-	-			-	-	70±43	0.77±0.21
Females								
19	3839	400			42	21	379	0.05
20	nd	nd			53	74	nd	Nd
21	4602	497			876	74	423	0.15
24	2857	154			181	22	132	0.14
26	2966	261			234	32	229	0.12
27	3640	238			287	42	196	0.18
28	4567	223			276	53	170	0.24
29	2714	182			175	16	166	0.09
Mean ±SE	-	-			-	-	242±43	0.14±0.02
Males								
19	9668	334			127	21	313	0.06
20	nd	nd			64	91	nd	Nd
21	13227	737			1274	53	684	0.07
24	9026	161			154	32	129	0.20
26	7197	191			159	11	180	0.06
27	9622	204			340	42	162	0.21
28	12316	176			541	85	91	0.18
29	6982	207			244	21	186	0.10
Mean ±SE	-	-			-	-	249±77	0.13±0.03

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Table 5. Values of G, D and NPM (d^{-1}) of *Arctodiaptomus salinus* in Lake Shira calculated from Eq.16 and Eq.17.

Daysof June	G	D	NPM	
			FromEq.16(with $\bar{y}_{(i)}$	From Eq. 17(with y_i*)
Nauplii				
19-21	0.473	0.443	0.044	0.006
21-26	0.316	0.285	0.010	-0.009
24-29	0.074	0.067	-0.002	-0.004
C1-4				
19-21	0.592	0.570	0.100	0.034
21-26	0.457	0.424	0.032	-0.008
24-29	0.144	0.133	0.006	0.0001
C5				
19-21	0.234	0.217	0.008	0.0001
21-26	0.117	0.054	0.0003	-0.004
24-29	0.067	0.021	0.001	0.00001
Females				
19-21	0.869	0.823	0.103	0.017
21-26	0.538	0.458	0.048	-0.002
24-29	0.399	0.343	0.023	0.005
Males				
19-21	0.823	0.771	0.049	0.023
21-26	0.516	0.479	0.020	-0.006
24-29	0.408	0.327	0.008	0.002
Population mean				
19-21	-	-	0.061±0.018	- (not calculated)
21-26			0.022±0.008	-
24-29			0.007±0.004	-

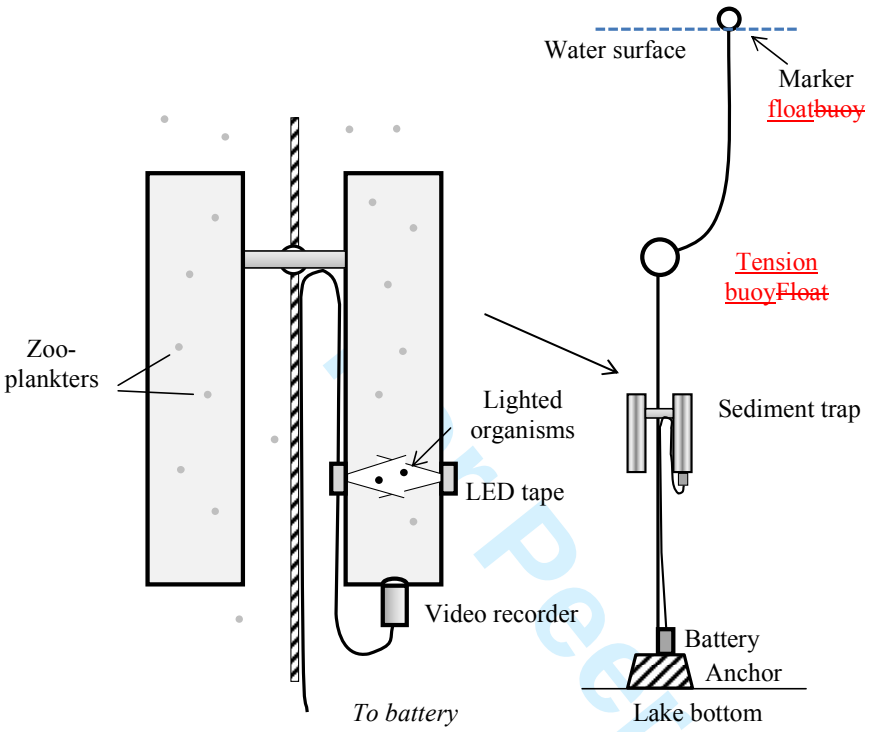


Fig. 1. Schematic of the sediment trap with digital video recorder and mooring system.

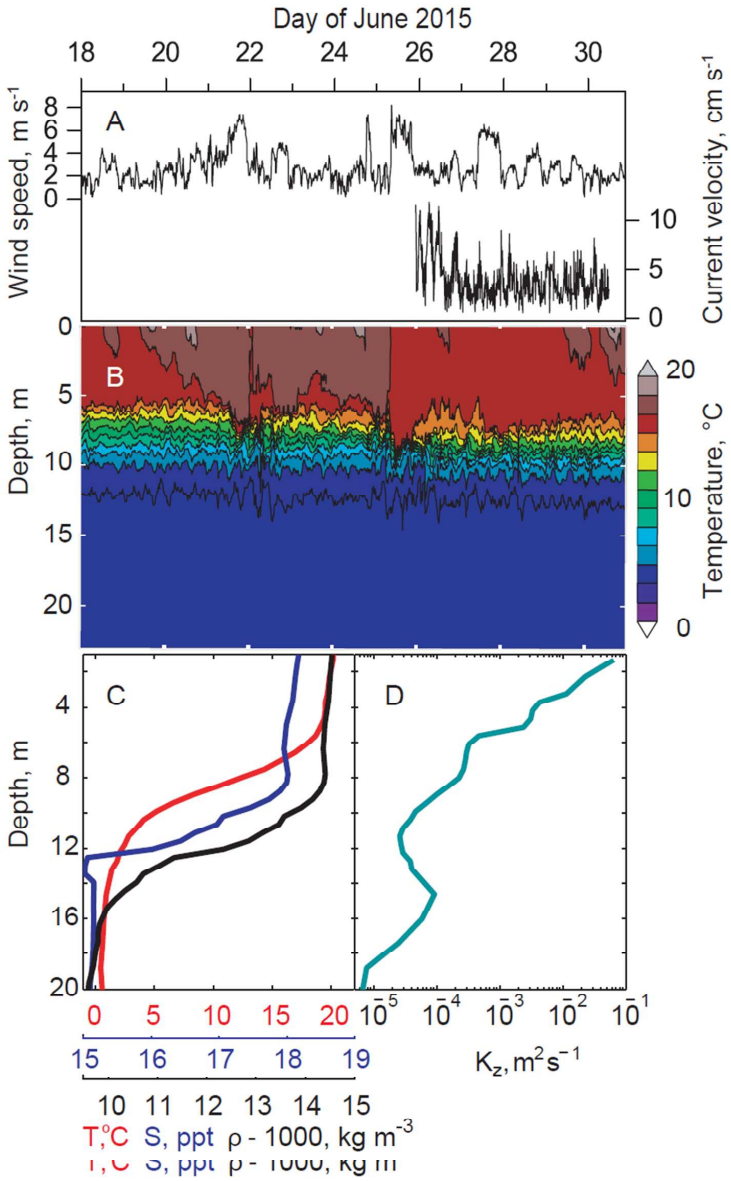
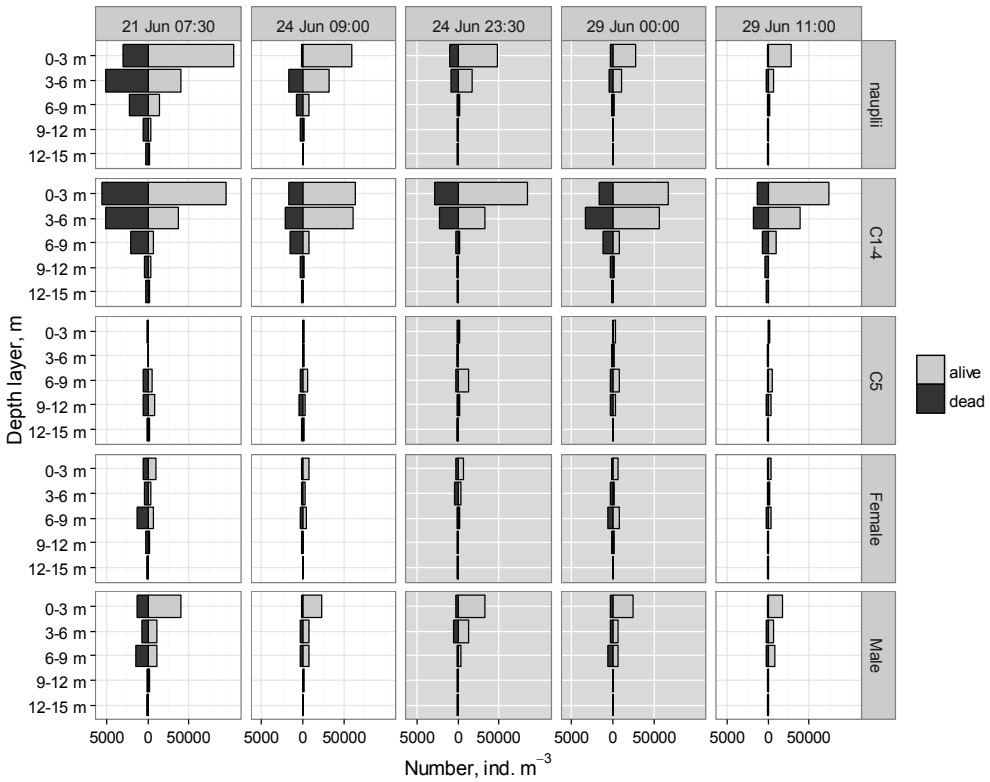


Fig. 2.(A) Wind~~Magnitudes of wind~~ speed, and current velocity~~velocities~~ at 14 m depth; (B) isotherms ~~evolution~~ during the study period~~; of the field experiments;~~ (C) mean vertical profiles of temperature, salinity and density; (D) Vertical profile of the turbulent exchange coefficient K_Z.


21 Jun 07:30
24 Jun 09:00
24 Jun 23:30
29 Jun 00:00
29 Jun 11:00
nauplii
C1-4
C5
Female
Male
0-3 m
3-6 m
6-9 m
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12-15 m
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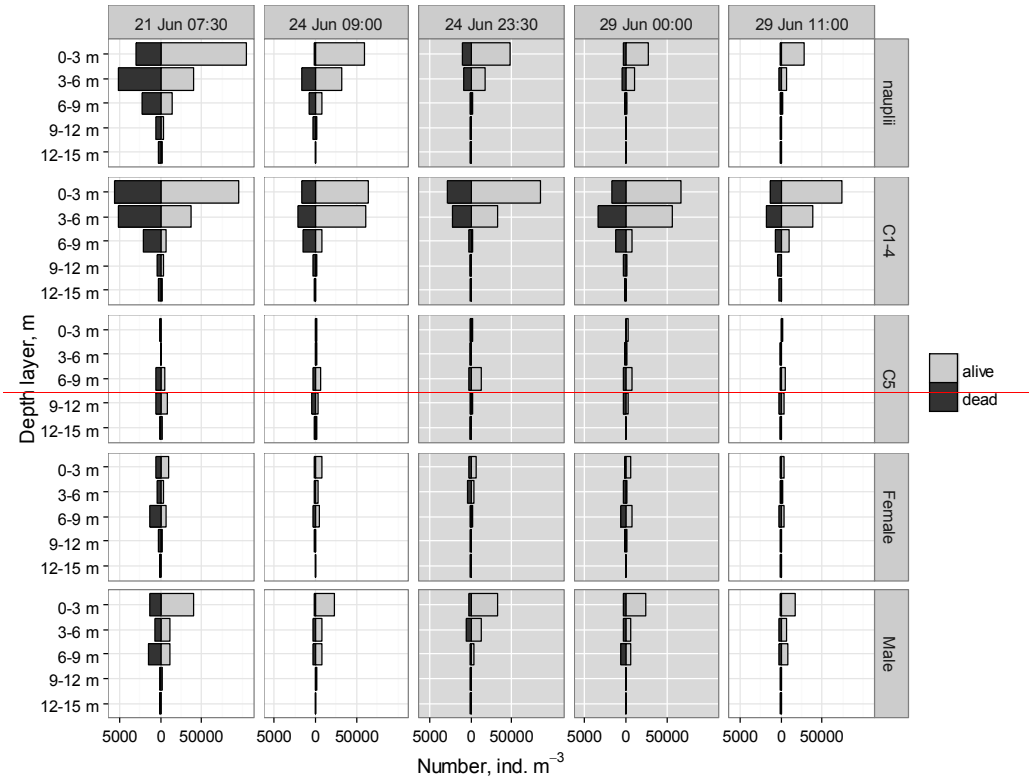

Fig. 3. Vertical distributions of live and dead *Arctodiaptomus salinus* in Lake Shira ~~Lake~~ on 21, 24 and 29 June 2015. The shaded panels correspond to the nighttime.

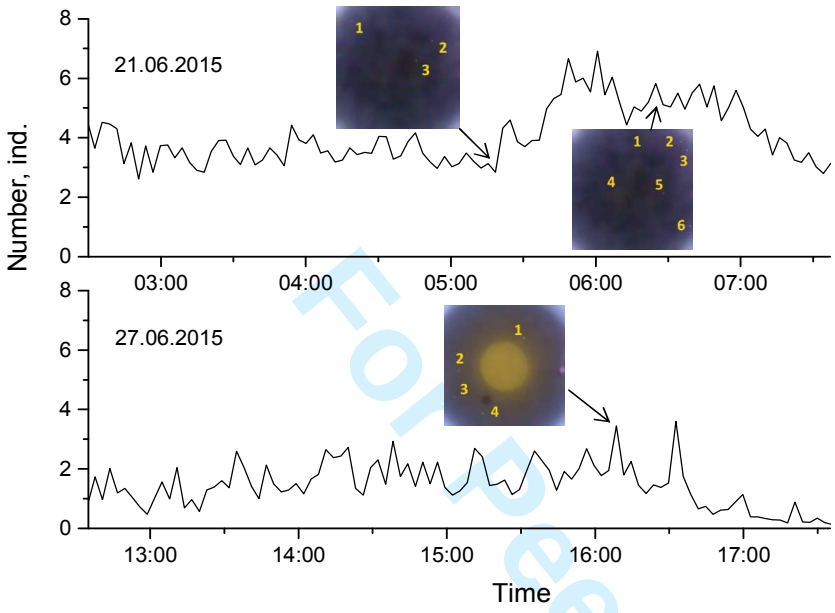

Fig. 4. Number~~Dynamics of a number~~ (as 10-min average) of *Arctodiaptomus salinus* in ~~field of video recorder vision in~~ the sediment trap detected by the video recorder on 21 June (nighttime) and 27 June (daytime). The numbers in the inserts mark~~figures marked~~ animals visible within~~on~~ the field of view.~~frames.~~

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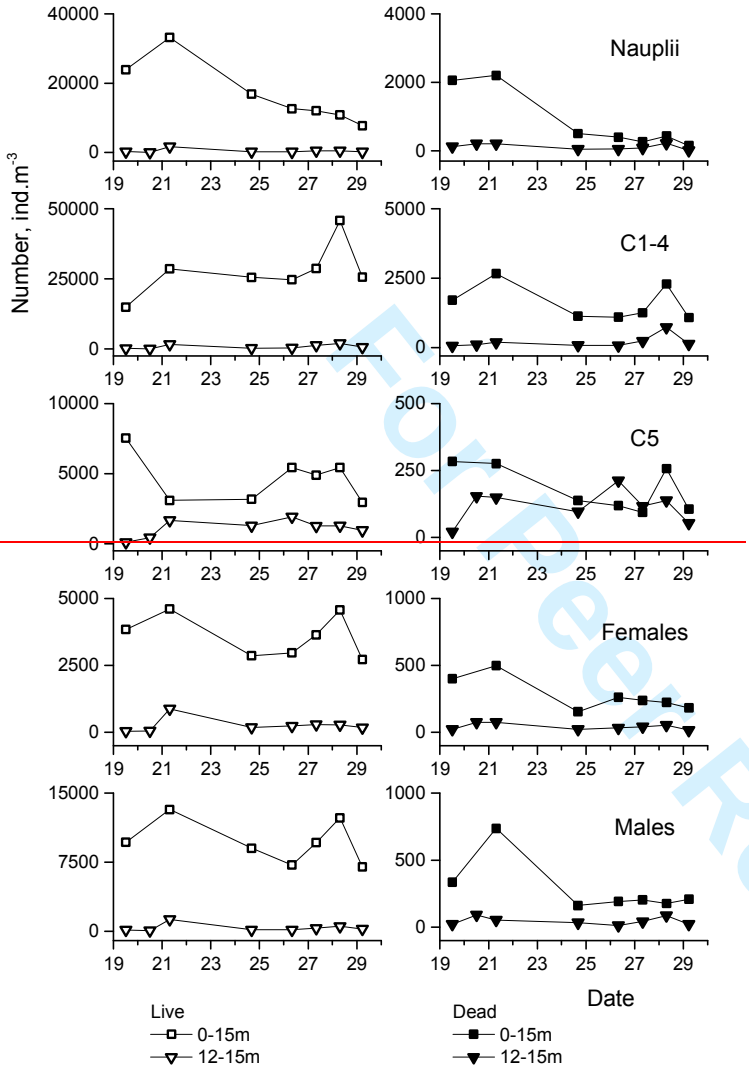

Fig.5. Weighted mean abundances (ind m^{-3}) of *Arctodiaptomus salinus* in 0-15 m water column and at trap depth, 12-15 m, in Shira Lake. For *m* calculation, data on 19, 21, 24, 26 and 29 June used.

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Table and Figure Legends

Table 1. Number of *Arctodiaptomus salinus* carcasses accumulated in sediment traps per day (Y, ind d^{-1}) and carcass abundances at trap depth, 12-15 m, average of 2-3 samples taken at the beginning and the end of daily trap exposure (v^*_{av}, ind m^{-3}) in Lake Shira ~~Lake~~ (for calculation of v^*).

Table 2. Number of *Gammarus lacustris* in the net column samples (ind. $sample^{-1}$), at trap depth and inside the traps, Lake Shira, ~~Lake,~~ 2015, dash – no samples.

Table 3. In situ sinking velocity (v^*, m d^{-1}) of *Arctodiaptomus salinus* carcasses calculated from Eq. 4 using data from Table 1 for Lake Shira. ~~Lake, means labeled with the same latter are not significantly different at P<0.05 after ANOVA post-hoc Fisher test.~~

Table 4. Weighted mean abundances (ind m^{-3}) of live and dead *Arctodiaptomus salinus* in 0-15 m water column and at trap depth, 12-15 m, in Lake Shira. For m calculations, data on 19, 21, 24, 26, 29 June were used (in bold).

Table 5. Values of G, D and NPM (~~values (m,~~ d^{-1}) of *Arctodiaptomus salinus* in Lake Shira ~~Lake~~ calculated from Eq.16 ~~Eq.6~~ and Eq.17 ~~Eq.8.~~

Fig. 1. Schematic of the sediment trap with digital video recorder and mooring system.

~~—~~Fig. 2.(A) Wind ~~Magnitudes of wind~~ speed, and current velocity ~~velocities~~ at 14 m depth; (B) isotherms ~~evolution~~ during the study period ~~of the field experiments;~~ (C) mean vertical profiles of temperature, salinity and density; (D) Vertical profile of the turbulent exchange coefficient K_Z.

~~—~~Fig. 3. Vertical distribution of live and dead Arctodiaptomus *salinus* in Lake ~~*salinus* in~~ Shira ~~Lake~~ on 21, 24 and 29 June 2015. The shaded panels correspond to the nighttime.

~~—~~Fig. 4. Number ~~Dynamics of a number~~ (as 10-min average) of Arctodiaptomus salinus ~~in field of video recorder vision~~ in the sediment trap detected by the video recorder on 21 June (nighttime) and 27 June (daytime). The numbers in the inserts mark ~~figures marked~~ animals visible within ~~on~~ the field of view. ~~frames.~~

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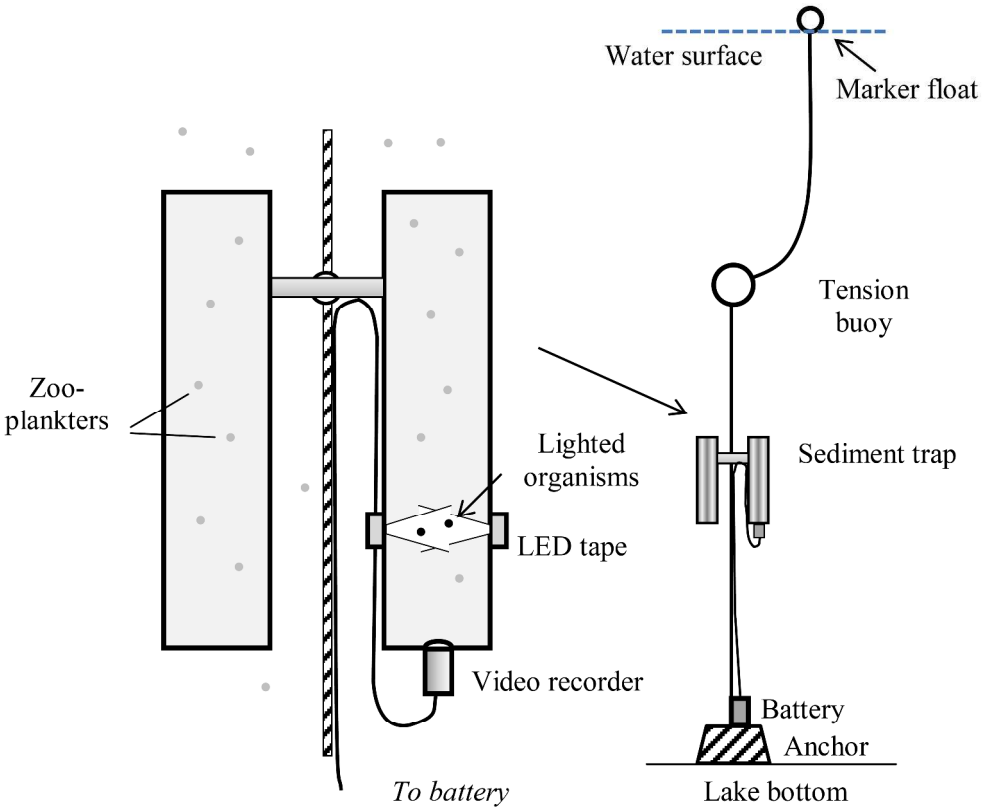

Fig. 1. Schematic of the sediment trap with digital video recorder and mooring system.

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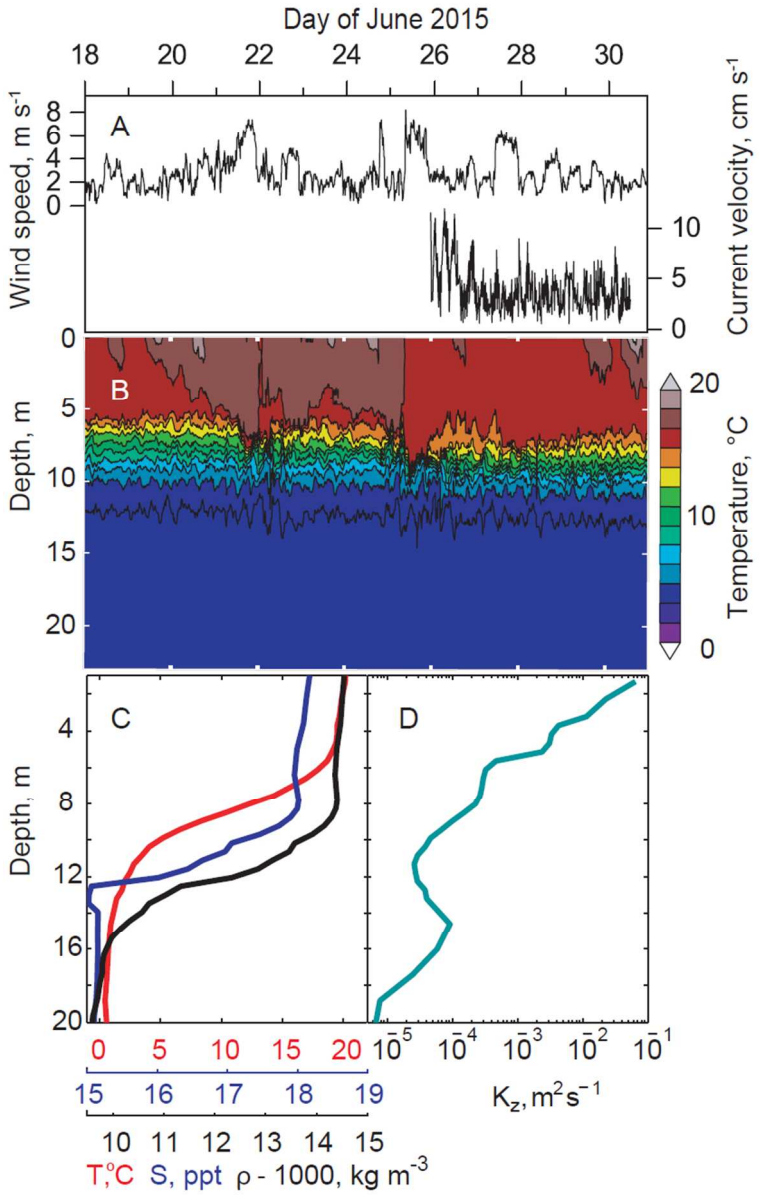

Fig. 2.(A) Wind speed, and current velocity at 14 m depth; (B) isotherms during the study period; (C) mean vertical profiles of temperature, salinity and density; (D) Vertical profile of the turbulent exchange coefficient KZ.

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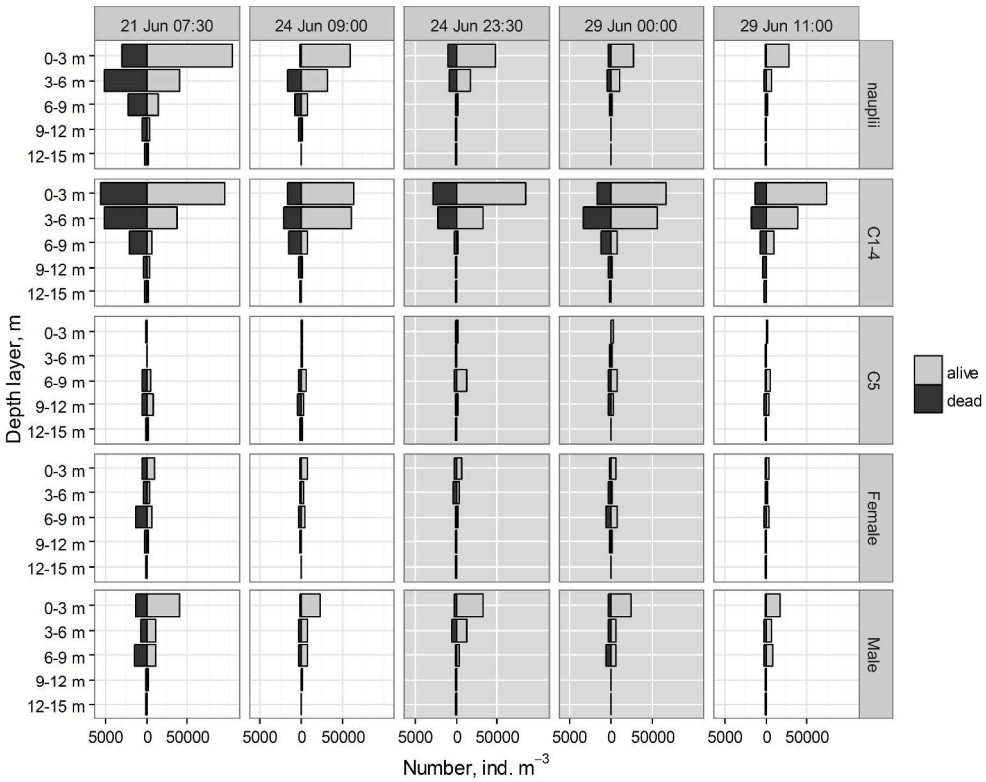

Fig. 3. Vertical distribution of live and dead ArctodiaptomussalinusinLake Shira on 21, 24 and 29 June 2015. The shaded panels correspond to the nighttime.

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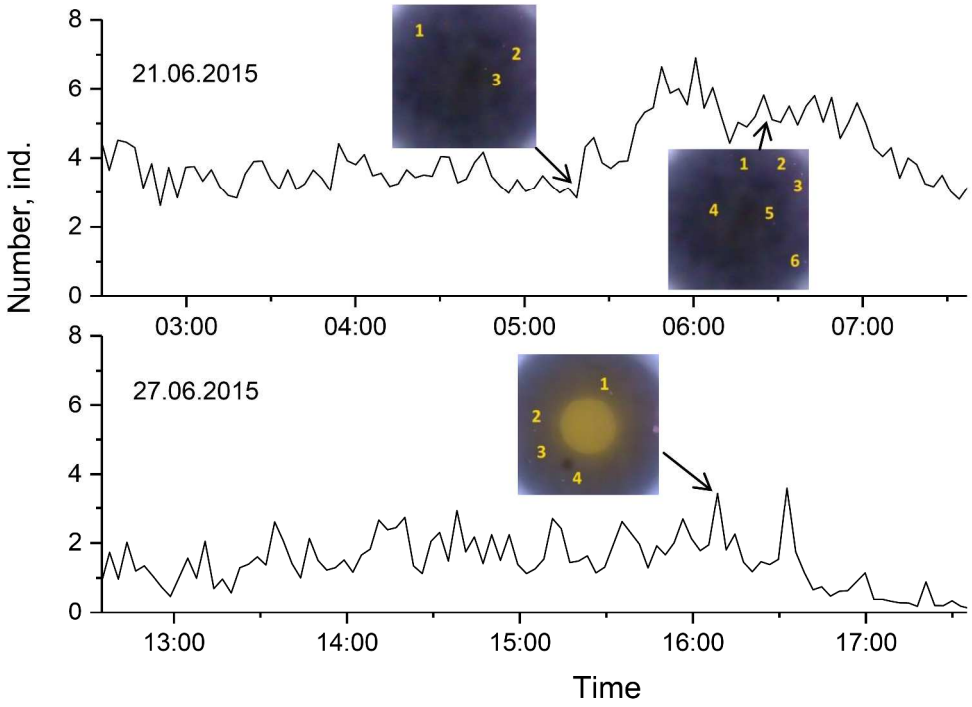

Fig. 4. Number (as 10-min average) of Arctodiaptomussalinusin the sediment trap detected by the video recorder on 21 June (nighttime) and 27 June (daytime). The numbers in the inserts mark animals visible within the field of view.

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